UNIVERSITY OF ALBERTA

VOCAL COMMUNICATION AND MOTHER-PUP INTERACTIONS IN THE SOUTH AMERICAN FUR SEAL, *Arctocephalus australis*.

BY

ALANA VIOLETTE PHILLIPS ©

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled VOCAL COMMUNICATION AND MOTHER-PUP INTERACTIONS IN THE SOUTH AMERICAN FUR SEAL, *Arctocephalus australis*, submitted by ALANA VIOLETTE PHILLIPS in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in ENVIRONMENTAL BIOLOGY AND ECOLOGY.

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ABSTRACT

Vocal communication and mother-pup behaviour of South American fur seals (*Arctocephalus australis*) in Peru were investigated. The vocal repertoire is large, and adult females produce threat calls more frequently than other fur seal species. Some of the potential factors influencing female aggression include social interactions, climatic conditions and disturbances by sea lions. To facilitate reunion with their pups, mother fur seals consistently return to the same area of the colony, while pups play an active role in the reunion process. The calls used between mothers and pups are sufficiently variable that recognition by vocal cues is likely. Mothers' vocalizations are more individualistic than those of pups, enabling pups to recognize mothers from a distance and thereby reduce the potential of injury from non-related females. Calls of pups are not acoustically similar to those of their mothers, suggesting that neither heritability nor imitation of mothers' calls affects pup vocal development.

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1. GENERAL INTRODUCTION

This thesis is an investigation of vocal communication and mother-pup interactions of South American fur seals, *Arctocephalus australis*, breeding at Punta San Juan, Peru. In this chapter, I will place that research within the context of the field of animal communication in general, and the social behaviour and vocal evolution of pinnipeds in particular.

1.1 Animal communication

Animal communication may be defined as the transfer of information between individuals or groups of individuals, resulting in behavioural changes that are beneficial to one or both participants (Green and Marler 1979). Information about the sender is broadcast via a variety of signals within the range of sensory adaptations of a species. Thus, signals may be visual (such as coloration, posture or motion), auditory (including vocalizations and noises produced by other sources), tactile, chemical or electric. Displays are stereotyped signals that have evolved in response to selective pressures for communication purposes. Other signals, such as pelage colour, may be unspecialized for communication or related to other functions, but supplement the information made available by displays. The diversity of signals among animals is tremendous; many examples are provided in reviews such as Smith (1977), Sebeok (1977), Marler and Vandenbergh (1979), Gould (1983) and Miller (1991).

Tinbergen (1953) suggested that the display behaviour of animals is simply an innate reflection of their underlying motivational state. Others have expanded on this theory, noting that many animal displays appear to be correlated with their affective state (Morton 1977, 1982; Scherer 1985; August and Anderson 1987). Alternatively, Smith (1977) argued that displays refer to broadly predictable messages describing the likelihood of future behaviour, such as the probability that the sender is receptive or seeks interaction, or that it will move or change its activity. In either case, broad messages are likely economical, since each can be employed in a variety of situations, allowing the context of the situation to play an important supplementary role in the receiver's ability to interpret the message and make an appropriate response. Context may include the external cues present in the situation of the display as well as prior experience and learning (Smith 1977). Signals which refer to specific referents are relatively uncommon, since they must be important enough to warrant their cost. For example, some primates and ground squirrels produce alarm calls which indicate whether a nearby predator is avian or terrestrial, as well as the appropriate defensive strategy to use, even though such calls may reveal the sender's location to the potential predator (Seyfarth *et al.* 1980; Cheney and Seyfarth 1990; Macedonia 1990; Slobodchikoff *et al.* 1991; MacWhirter 1992; Macedonia and Evans 1993).

For species that can occur in large groups, communication is particularly important for maintaining social organization and group cohesiveness. In groups, fighting and fleeing are potentially costly to individuals and typically disruptive to the animals' activities, so agonistic displays (such as the growls, lunges and open-mouth threats of many mammals) that avoid more overt interaction are common. Displays indicating threat, appeasement and territorial ownership enable participants to resolve conflicts while avoiding the risk of injury (Smith 1977; Archer 1988). Courtship displays and elaborate mating and post-copulatory behaviour may also be present in social animals. Communication between parents and offspring serves a variety of roles, including warning of predators and maintaining parent-offspring bonds (Holmes 1990). In species that live in complex social groups and interact daily with several individuals, signals that provide the ability to distinguish kin from non-kin, or even to discriminate among individuals, can be advantageous (for reviews see Colgan 1983; Holmes and Sherman 1983; Hepper 1986; Porter 1987; Waldman 1988).

1.2 Communication and breeding behaviour in the pinnipeds

The pinnipeds[1] are a diverse group of marine carnivores found in most regions of the world, consisting of 33 extant species within the Families Phocidae (true or earless seals), Otariidae (fur seals and sea lions, or eared seals) and Odobenidae (walrus). Generally, pinnipeds are characterized by adaptations for aquatic feeding, such as a streamlined body form, a reduction of external projections, a layer of blubber and numerous adaptations for diving. However, unlike the Cetacea (whales and dolphins) and Sirenia (dugongs and manatees), seals are not adapted for a fully aquatic existence, since seal pups are born and nursed out of water, either on land or ice surfaces (Scheffer 1958; King 1983).

---

[1] Throughout this work, I use "seal" and "pinniped" synonymously, and use the term "true seals" to distinguish the phocids. Taxonomy follows that of the IUCN/SSC Seal Specialist Group (1993).

The sensory mechanisms of pinnipeds are largely adapted for underwater foraging and predator evasion, but numerous adaptations exist for communication both in air and underwater (for reviews see Winn and Schneider 1977; Schusterman 1981; Miller 1991; Renouf 1991b). Like other mammals adapted for vision in low light levels, pinniped eyes are large, with a spherical lens to compensate for the refractive index of sea water. Seals are not known to distinguish colours, and are myopic (short-sighted) in air, so visual communication tends to be limited to body size and posture, flipper positioning and facial expressions (such as the ubiquitous "open-mouth display") (Stirling 1971; Miller 1975). Since the nares are closed while diving, olfaction is used only in air. Odour is likely an important cue in territorial behaviour, advertisement of estrus, recognition of individuals and maintenance of the mother-pup bond (Miller 1991; Renouf 1991b). Tactile communication may also be important. Pinnipeds have highly developed vibrissae, which are used primarily for detecting prey but are also involved in social behaviour such as boundary displays and mother-pup interactions (Miller 1975, 1991; Renouf 1991b). Other forms of social touching may include nuzzling, biting and passive body contact (Miller 1991).

On land, vocalizations may be the most important means of communicating, since they can be produced and heard over relatively long distances (Miller 1991). Hearing and sound production are well developed for both air and water, with a typical optimal range of 2-20 kHz in air (Schusterman 1981). Seals produce a range of vocalizations, including low, harsh sounds (e.g. growls, grunts); loud, high-pitched calls (e.g. "pup-attraction calls"; "barks" of male California sea lions, *Zalophus californianus*); long, melodious songs produced underwater by male Weddell seals (*Leptonychotes weddellii*); and bell-like sounds of walruses (*Odobenus rosmarus*) (e.g. Peterson and Bartholomew 1969;

Stirling 1971; Stirling and Warneke 1971; Thomas and Kuechle 1982; Stirling *et al.* 1987; Cleator *et al.* 1989; Miller and Job 1992; Ballard and Kovacs 1995).

Communication among pinnipeds is probably most important during the reproductive season, because outside of the breeding period seals tend to forage independently and may disperse variable distances while pelagic. This might limit their potential for finding members of the opposite sex with which to mate if they remained pelagic. Thus, the combination of offshore marine foraging and terrestrial breeding has significantly influenced the evolution of the social systems of pinnipeds, resulting in strong selective pressures for seals to congregate at the same time and place to reproduce (Bartholomew 1970; Stirling 1975, 1983).

The available habitat for parturition, nursing and copulation also affects the type of breeding system a particular seal species is likely to exhibit. Most phocid species copulate in the water and give birth on ice, where there is abundant habitat and relatively easy escape from predators. Females remain relatively dispersed during the breeding season, and lactation is typically short, ranging from 4 days to about 3 weeks, to ensure that pups are weaned before the ice breaks up; these factors prevent males from monopolizing large groups of females. Thus, ice-breeding seals tend to exhibit a low level of polygyny, in some species tending towards serial, or seasonal, monogamy (Bartholomew 1970; Stirling 1975, 1983; Le Boeuf 1991). Additionally, mothers and pups are rarely separated, so the need for behaviours that maintain contact between mothers and offspring tends to be negligible (Tedman and Bryden 1979; Kovacs 1995). For species that give birth and copulate on land (including the otariids, the two species of elephant seal (*Mirounga* spp.) and the grey seal (*Halichoerus grypus*)), females tend to congregate in the limited number of coastal or island habitats which offer protection from land-based predators and from the elements. This has led to the development of a gregarious, polygynous mating system, in which males compete for territory in the areas where the greatest numbers of females occur (Bartholomew 1970; Stirling 1975, 1983; Boness 1991; Le Boeuf 1991). However, breeding in dense colonies also incurs numerous disadvantages, including increased pup mortality due to the combined effects of disease, trauma inflicted by adults, and disruptions resulting in separation of pups from mothers (Le Boeuf and Briggs 1977; Bowen 1991).

Maternal care, mother-pup interactions and requirements of pups are similar among otariid species (Bartholomew 1959; Peterson and Bartholomew 1967; Sandegren 1970; McNab and Crawley 1975; Trillmich 1981; Schusterman *et al.* 1992; see also reviews in Gentry and Kooyman 1986; Bowen 1991). Mothers give birth to a single pup which they attend continuously for five to ten days before coming into estrus. A strong bond appears to be formed during the perinatal attendance period, as mothers and pups remain in close contact and vocalize frequently to each other. After copulation, mothers depart for sea and thereafter alternate between nursing their pup on land and foraging at sea. Although the length of attendance and foraging periods varies among species, the relatively long nursing period of most otariid species means that reunion between mothers and pups occurs frequently (Gentry and Kooyman 1986). Upon returning to the colony, mothers appear to locate and recognize their pups using a combination of geographical, visual and vocal cues, and a final olfactory check (Bartholomew 1959; Trillmich 1981). While separated from their mothers, pups risk injury from other females, which do not tolerate unfamiliar pups and will bite or throw any that approach too closely. This type of aggression by females is common among colonially breeding pinnipeds and is exacerbated by high densities (Le Boeuf and Briggs 1977; Christenson and Le Boeuf 1978; Boness *et al.* 1982).

Breeding and maternal behaviour of otariids are further affected by factors such as latitude, food availability and environmental stability (reviewed in Gentry and Kooyman 1986; Renouf 1991a; Boness and Bowen 1996). For seals breeding in subpolar regions, available food resources are predictable and abundant but restricted to a brief period of a few months. Thus, pups tend to be born synchronously, to grow rapidly and to be weaned by around four months of age. In contrast, tropical species inhabit warm equatorial water which is low in productivity, so seals must rely mainly on the small areas of productive upwelling around islands and coastlines. Additionally, these equatorial regions are subjected to a substantial degree of environmental uncertainty, in particular, the El Niño Southern Oscillation (ENSO) events which occur at irregular intervals and cause suppression of the cold, nutrient-rich upwelling zones in the eastern Pacific Ocean, thereby significantly reducing the seals' food supply. Thus, in tropical species, food availability and other environmental conditions may cause the age at weaning to vary from five to 36 months (Trillmich and Ono 1991). This flexible maternal strategy is advantageous because in poor years, females may continue investing in the young of the previous year to ensure that it survives to weaning, rather than investing in a new pup each year. Frequently, however, the prolonged period of pup dependency may result in offspring from consecutive years being reared simultaneously, resulting in sibling competition and a substantial energy load on the mother (Bonner 1984; Gentry and Kooyman 1986; Oftedal *et al.* 1987).

Thus, communication is particularly important for otariids, to establish and maintain the territorial structure of the breeding colony, to minimize injuries due to aggression, and to maintain spacing between individuals. Mothers and pups must also be able to communicate effectively in order to locate and recognize each other, and to maintain close association throughout the lactation period (Winn and Schneider 1977; Miller 1991).

1.3 Breeding behaviour of the South American fur seal in Peru

Fur seals include eight extant species within the genus *Arctocephalus*, as well as the northern or Alaskan fur seal, *Callorhinus ursinus*. Currently, these species are distinguished primarily by their geographic range, and secondarily on morphometric and behavioural characteristics such as vocalizations; however, the interrelationships of the eight species are still under review (Repenning *et al.* 1971; Stirling and Warneke 1971; King 1983; Lento *et al.* 1997). The Arctocephaline fur seals are widespread in cold waters throughout the southern hemisphere, ranging from subpolar habitats (Antarctic fur seal, *A. gazella*, and subantarctic fur seal, *A. tropicalis*) to temperate (Australian/South African fur seals, *A. pusillus*, and New Zealand fur seal, *A. forsteri*) and tropical climates (South American fur seal, *A. australis*, Galapagos fur seal, *A. galapagoensis*, Juan Fernandez fur seal, *A. philippii*, and Guadalupe fur seal, *A. townsendi*) (Repenning *et al.* 1971; Bonner 1981; King 1983).

South American fur seals are similar to other tropical species in their morphology, behaviour and ecology. The species breeds in colonies along the southern coasts of South America from northern Peru around to Uruguay, and including the Falkland Islands (Majluf and Trillmich 1981; Majluf 1987a,b; Vaz-Ferreira and Ponce de Leon 1987). There are approximately 20,000 fur seals in Peru, concentrated in five main colonies between 15°S and 18°S where coastal upwellings occur. The species feeds primarily on anchovy (*Engraulis ringens*), sardine (*Sardinops sagax*) and other small schooling fish (Majluf and Trillmich 1981). Humans are the most important competitor for food resources, while fishermen and poachers also contribute to significant fur seal mortality. Non-human predation is not considered an important factor in overall mortality, because sharks and killer whales (*Orcinus orca*) are rarely seen off Peru (Majluf 1987b). However, South American sea lions (*Otaria byronia*) may account for up to 5% of juvenile deaths at specific locations (Harcourt 1992; Majluf 1992).

The breeding ecology of fur seals in Peru has been described by Majluf (1987a, 1992), Harcourt (1990) and Parlane (1997). Adult males (90-150 kg) are reproductively active between the ages of nine to fourteen, while females (30-90 kg) may produce pups from four to twenty years of age. Although adult females are present year-round, the reproductive season begins in late September with the arrival of mature males that establish territories in sites offering shade and access to water. Male mating success is variable, but males that are successful in maintaining territories may copulate with several females during a season. Pups are born between October and December, with the peak of pupping in November (Majluf 1992). The perinatal attendance period typically lasts eight to ten days. Mothers come into estrus about ten days after the pup is born, and depart for sea within a day after copulation. The attendance cycle typically consists of foraging at sea for up to five days at a time, alternating with nursing on land for two to three days (Majluf 1987a). The territorial structure breaks down at the end of December, when most of the males disperse. Pups may start to leave the beach for significant periods of time by late April, although weaning does not begin until May. Although many pups are weaned at approximately six to eight months, mothers are often seen suckling yearlings or even two-year-olds (Trillmich *et al.* 1986; Majluf 1987a, 1991, 1992).

As in other tropical species, thermoregulation has a significant influence on the social system and reproductive behaviour of South American fur seals (Gentry 1973; Francis and Boness 1991). With their thick fur and layer of blubber designed for swimming in cold waters, seals have a limited capacity for dissipating heat. Thus, thermal stress and overheating occur rapidly when animals on the dry beach are subjected to intense solar radiation, causing the seals to make behavioural adjustments such as withdrawing into shaded areas, immersing themselves in water or moving to the tidal area (Trillmich and Majluf 1981; Limberger *et al.* 1986). In Peru, females and pups spend the night above the high tide line, resting and nursing where there is space for them to spread out. In the morning, as soon as insolation reaches a critical level, females begin to move down toward the tidal area, carrying their pups or calling to them as they move through the colony. Once in the tidal area, females compete for the limited access to water and shade provided there. In the late afternoon, the migration is reversed, as females move up the beach away from the tide line. Since movements in response to thermoregulatory stress are a daily event and females have been found to cluster in predictable locations during the day, only males that defend territories in these areas are reproductively successful (Majluf *et al.* 1996).

Fur seals in Peru are subjected to additional factors that are unique to their situation. Centuries of human disturbances such as poaching and harassment by fishermen have limited the available space for breeding, resulted in high densities in the few remaining colonies (Majluf 1992). Furthermore, since South American sea lions are also present at most of the colonies, competition for space and pressure to protect pups from sea lion predation have tended to restrict fur seals to those beaches with steep, rocky shores and moderate to heavy surf. In contrast, other species of fur seal are able to take advantage of terrain bordering the breeding beaches for nursing pups and maintaining greater spacing between individuals (e.g. tussock grass: New Zealand, Antarctic and Galapagos fur seals; sand dunes, South African fur seal (Stirling 1971; Croxall and Gentry 1987)).

A number of factors therefore influence the ability of adult female South American fur seals to successfully rear offspring. Most importantly, the density of the colonies combined with the roughness of the terrain and the level of thermal stress experienced by the animals results in levels of female aggression, and subsequent pup mortality, higher than has been recorded for any other otariid species (Harcourt 1991, 1992; Majluf 1992). Therefore, communication is expected to be important to South American fur seals for minimizing overt aggression, conserving energy in the tropical heat, and maintaining contact between mothers and pups.

1.4 Objectives and thesis format

In this study, I examine the vocal communication and mother-pup interactions of South American fur seals in Peru, and use comparative analyses to explore how both have adapted to the specific environmental and social pressures operating on the species. First, I describe the vocal repertoire of the species and compare it to that of others within the genus *Arctocephalus* (Chapter 3). I then explore some of the potential factors influencing female aggression at Punta San Juan (Chapter 4). Next, I investigate the behavioural processes used by mothers and pups to facilitate reunion and maintain recognition. Do mothers employ a variety of behaviours to ensure that reunion is achieved quickly (Chapter 5)? Are the calls used between mothers and pups sufficiently variable that recognition would be possible (Chapter 6)? Since female aggression is a major cause of pup mortality, female vocalizations are likely to be highly individualistic, to enable pups to recognize them from a distance and thereby reduce the potential of injury from other females. Finally, I examine the mechanism by which pups might acquire their individual calls, hypothesizing that pup calls would share structural features with calls of their mothers (Chapter 7). In chapter 8, I summarize the main conclusions of this study and identify some topics that might be investigated further. As this thesis is written as a series of independent chapters, there is some overlap in the material presented.

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2. GENERAL MATERIALS AND METHODS

2.1 Description of the study site - Punta San Juan, Peru

The study was conducted at Punta San Juan (15°22'S, 75°12'W), one of the main breeding sites for South American fur seals in Peru. The 54 ha. peninsula (Figure 2-1) is surrounded by a concrete wall, and has been designated a protected area for breeding colonies of guano-producing birds, notably Guanay cormorants (*Phalacrocorax bougainvillii*), Peruvian pelicans (*Pelecanus thagus*) and Peruvian boobies (*Sula variegata*). Fortuitously, the lack of human disturbance also provides a safe breeding environment for fur seals, sea lions, Humboldt penguins (*Spheniscus humboldtii*) and occasional migratory shorebirds, all of which would otherwise be restricted to offshore islands (Majluf and Trillmich 1981). In years not affected by El Niño events, approximately 2,000 - 3,000 South American fur seals are typically present at Punta San Juan during the breeding season, comprising about 15% of the Peruvian population of the species (P. Majluf, unpubl. data). Fur seals and sea lions inhabit most of the bays in the reserve, although the two species do not intermix; fur seals occupy steep, rocky beaches with boulders and tidepools, while sea lion colonies occur on relatively flat, sandy or pebbly beaches.

Research for this study was conducted during the breeding seasons in 1994 (Nov 12 - Dec 12) and 1995 (Sept 26 - Dec 19), which overlapped with the annual peak of pupping activity (Majluf 1987, 1992). Times of day refer to Peruvian Standard Time (GMT-5).

2.2 Description of beach N4

The majority of the research for this study was conducted at beach N4 (Figure 2-1), a mostly sandy beach sheltered at the south-west end by an arched headland which curves around sharply to the north (Figure 2-2). A small colony of fur seals breeds in an area of boulders and tidepools in this sheltered region (Figures 2-2, 2-3). Males maintain territories in the boulder/tidepool area, while females compete for access to shade and water during the day. At night, females and pups move up the beach to the pebbled area.

When departing to or returning from sea, most females entered the larger tidepool in the western region of the colony (Figure 2-3).

The breeding colony was newly established compared to other colonies at Punta San Juan; pups had only been present since 1992 (P. Majluf, unpubl. data). During the two years of this study, the colony typically consisted of 10-12 territorial males, 120-160 adult females, 100-140 pups and 10-20 juveniles, sub-adults and non-territorial males combined at the peak of the breeding season (see Figure 3-1). More females and pups were present in 1995 than in 1994 (Figure 3-1).

The colony size (large enough for the sample to be representative, but low enough that individuals could be observed and recorded), presence of a downwind observation point on the headland and minimal wind and wave noise made beach N4 an ideal site for a study of behavioural interactions and vocalizations of the South American fur seal.

2.3 Tagging and handling

Many individual fur seals have been tagged at Punta San Juan (primarily on beach S3), enabling data to be collected from animals of known age, sex and reproductive history. For this study, additional females and pups were tagged on beach N4 in both breeding seasons, using methods described in detail by Majluf and Goebel (1992). Briefly, mothers with newborn pups were selected, and approached with a 5 m bamboo pole affixed with a noose, which was slid around the pup and twisted; the pup was then pulled away from its mother, inciting her to chase it up the beach. The female was then caught using a hoop net, weighed using a 100 kg Pesola spring balance suspended from a tripod, and restrained on a board. Pups were weighed in a nylon mesh bag using a 20 kg Pesola spring balance. Females and pups were tagged on the distal insertion of each foreflipper, using Allflex Medium tags which were marked with three- or four-digit codes readable from the clifftop with binoculars (for example, see Figure 3-7f). The seals were further marked by trimming a number or similar mark into the guard hair layer of the pelt and bleaching the underfur with Clairol Born Blonde hair dye. After tagging, mothers were reunited with their pups and released at the capture location.

At beach N4, 16 mother-pup pairs and three solitary pups (1994), and 23 mother-pup pairs and four solitary pups (1995) were captured and tagged. The tags on three females first caught in 1994 were replaced (due to poor condition) when they were re-captured with new pups in 1995. The date of birth was known only for pups born to tagged mothers. For all other pups, the date of birth was estimated as eight days before the mother's copulation date or nine days before the mother first left the colony to go to sea (obtained from attendance records). These estimates were based on an average copulation date of eight pup days (P. Majluf, unpubl. data) and observations in the field that mothers typically leave for their first foraging trip the day after copulation. Additionally, the presence of an umbilicus when the pup was captured for tagging was assumed to indicate a maximum age of two days; thus, the age of a pup for which female copulation or departure dates were unknown could be estimated to a range bounded by the birthdate of the first pup on the beach that season and the date that the pup in question was tagged.

Tagged animals for which data were recorded during this study are listed in Appendix A.

2.4 Behavioural observations

At beach N4, a bench (1994) or hut (1995) located on a 10 m high cliff downwind of the colony allowed behavioural observations and recordings to be made without disturbing the animals (Figure 2-2). Other observations and recordings were made from a hut at beach S3 (Figure 2-1), where long-term studies of female reproductive ecology are on-going (Majluf 1987), and on both beaches during tagging activities. Tags were read using 8x35 or 10x40 binoculars or a 15 - 60 power zoom telescope.

A census of territorial males, adult females and pups was conducted daily between 0600 - 0700 at beach N4 (See Figure 3-1). In 1995, yearlings were also counted. To monitor attendance patterns and movement of tagged females, tags were read three times daily, between 0600 - 0700, 1200 - 1300 and 1700 - 1800. I also recorded the time of arrival of any tagged mothers returning to the colony from sea. For tagged mother-pup pairs, mothers were recorded as "present" or "absent"; pups were always present unless they died before the end of the study. For solitary tagged pups (mother not tagged), mothers were recorded as "present" only if the marked pup was seen in close association with a non-aggressive female. If no female was seen near the pup or there were insufficient contextual cues to determine whether a nearby female was the pup's mother, I recorded "pup alone", since I could not conclude whether the pup's mother was at sea or merely elsewhere in the colony.

2.5 Recording techniques

Recordings were made onto Maxell XLII 60 minute cassettes using a Marantz PMD430 cassette recorder and a Sennheiser K3N / ME 88 directional microphone with the filter set to Position III to reduce wave and wind noise. A running commentary was recorded on a separate channel using a Sony F27 microphone, a Genexxa Ultra-Miniature Tie Clip microphone, or (when the microphones malfunctioned) a pair of Sony MDR-E225 stereo headphones connected to the microphone input. Each recording session was prefaced on tape with the date, time, tape counter number, location, equipment settings (including recording levels) and weather conditions (when unusual; see Chapter 4). To facilitate management of the recordings and to document the types of recordings accumulated for each individual or research topic, a catalogue of all recording sessions was also maintained. For each session, the catalogue included tape and counter numbers, start and end time, equipment used, recording levels, age-sex class of emitting animal (and tag number when applicable), quality and quantity of calls and additional comments.

Focal animals were chosen *ad libitum* according to the suitability for recording. Priority was given to tagged animals that were clearly visible, and in particular to tagged mothers returning from foraging trips. The need to optimize recording conditions in order to obtain high quality recordings for subsequent acoustical analyses led to a bias towards individuals that produced loud calls and to situations with low background noise; however, some of the tagged animals vocalized so infrequently that, of necessity, some recordings were made under less than ideal conditions. The recording session ended when the focal animal became silent or disappeared from view. During the recording session, every call of interest was identified simultaneously on the commentary channel, and sex and age class of the animal making the call was noted. Whenever possible, the context of the calls was also described in the on-going commentary. Background or poor quality calls were generally not identified, especially since these were less likely to be given by a focal animal.

Most of the calls were recorded from the cliff-top bench or hut at N4, a diagonal distance of approximately 15 m. Additionally, during tagging activities on beaches N4 and S3, it was often possible to obtain recordings directly from animals on the beach, from distances ranging from 0.1 - 3.0 m.

2.6 Acoustical and statistical analyses

Spectrographic analyses were conducted using the SIGNAL/RTS sound analysis package (Engineering Design, Belmont, Mass.). Details on sampling rates, spectrogram calculations etc. are provided in each chapter.

All statistical analyses were made with SPSS for Windows v. 6.1 (SPSS Inc., Chicago, Il.), except for the likelihood ratio tests which were made using STATXACT (Cytel Software Corp., Cambridge, Mass.). STATXACT uses Monte-Carlo sampling of the raw data (using 5,000 replications) to generate a sample distribution against which the test statistic can be compared. This type of randomization test is preferable to both parametric and non-parametric techniques for data which are sparse or non-normally distributed (Crowley 1992; Potvin and Roff 1993; Adams and Anthony 1996). The level of significance (α) used throughout is 0.05.

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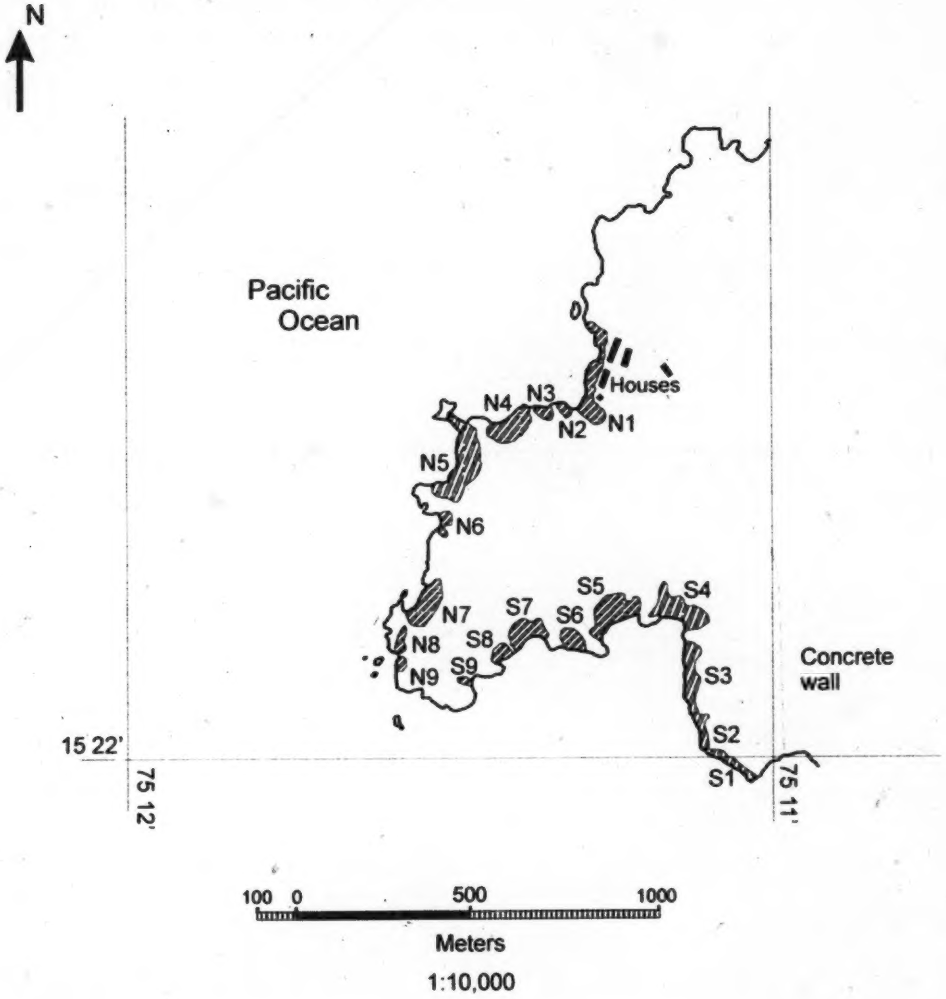
N
Pacific
Ocean
Houses
N1
N2
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N4
N5
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S5
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S8
S9
Concrete
wall
15 22'
75 12'
75 11'
100 0 500 1000
Meters
1:10,000

Figure 2-1. Aerial view of Punta San Juan, indicating the beaches where fur seals and sea lions are found (adapted with permission from Majluf 1987). Prefixes indicate northern (N) and southern (S) beaches. The guano-producing bird colonies are mostly situated on the peninsula between beaches N6 and S6.

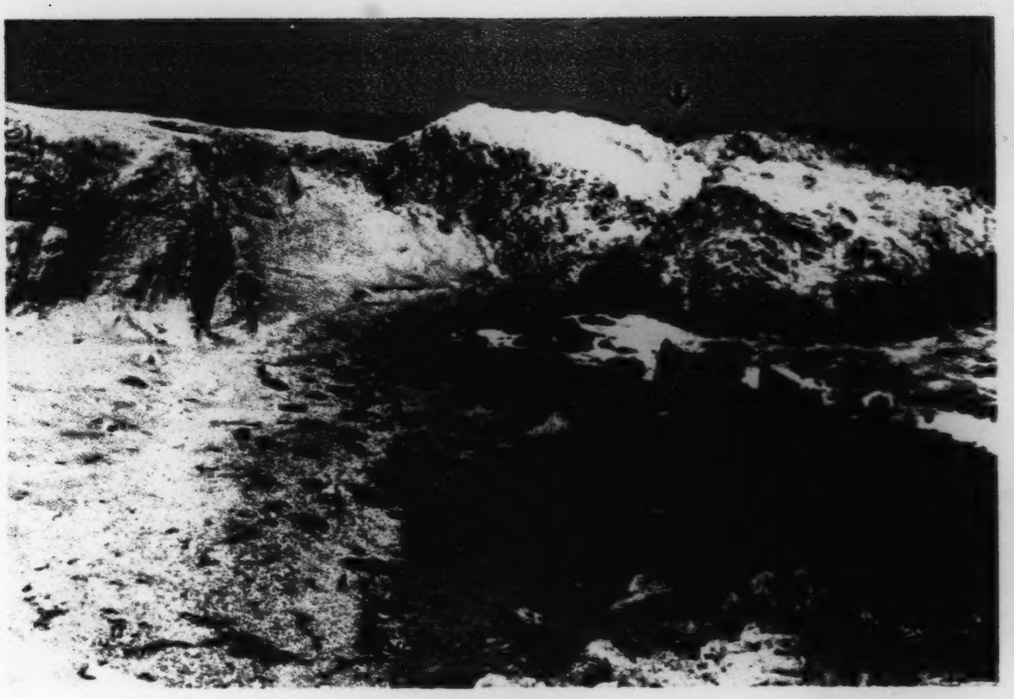

Figure 2-2. View of beach N4, looking west toward the breeding colony. The point from which most observations and recordings were made is indicated with an arrow.

Figure 2-3. View of the breeding colony at beach N4 from the observation point, at midday and low tide. Note the distribution of fur seals within the tidepool area. Access to and from the sea is to the left of the photograph.

3. VOCAL REPERTOIRE OF THE SOUTH AMERICAN FUR SEAL AT PUNTA SAN JUAN, PERU.

3.1 INTRODUCTION

A species' vocal repertoire describes all of the communicative sounds made by each sex and age class of a species. As such, it represents a vocal ethogram, and may be used in conjunction with other behavioural data to infer the meaning or social context of each signal. In studies of vocal communication, it is important to describe as much of the range of acoustical signals as possible, rather than only certain call types (e.g. Eisenberg *et al.* 1975; Barclay *et al.* 1979; Kroodsma 1982; Conner 1985; Ford 1989; Harcourt *et al.* 1993).

To date, the vocal behaviour of the South American fur seal (*Arctocephalus australis*) has received little attention. Some of the calls made by this species were described verbally by Vaz-Ferreira (1956, 1971), and by Trillmich and Majluf (1981) who also produced sound spectrograms for some of the more common vocalizations. However, both studies were based on a small sample size and did not include all call types. Knowledge of the vocal repertoire is essential for the questions I will be addressing in subsequent chapters (4-7). Before being able to investigate call variation among individuals, I first require a comprehensive summary of the range of sounds produced by South American fur seals. More specifically, I need to know what calls are made by females and pups, and which of these are used specifically in mother-pup interactions, before being able to investigate the hypothesis that individual variation in one may be important to recognition by the other. In this chapter, I document the vocal repertoire of the South American fur seal in Peru during the breeding season, and compare it to information reported for other *Arctocephalus* species.

3.2 MATERIALS AND METHODS

3.2.1 Terminology

A glossary of the acoustic terms used in this thesis is provided in Appendix B. I use the nomenclature of Stirling and Warneke (1971) or terminology coined in the field (Phillips and Stirling, unpubl.). With the exception of the pup-attraction call (see below), I differ from Stirling and Warneke (1971) and from Trillmich and Majluf (1981) by not categorizing calls into "male" or "female" vocalizations.

Miller (1991), Miller and Job (1992) and Insley (1992) have argued that the terms "pup-attraction call" and "female-attraction call" may be misrepresentative, particularly when pairs call during physical contact, and exclude interactions between mothers and yearlings. The term "female-attraction call" is especially ambiguous, since it distinguishes neither the sender (which could be an adult male attempting to copulate) nor the recipient (which could be any female of any age). However, due to the prevalence of these terms in the literature, I have retained them in this thesis. I use "pup-attraction call" to refer to non-agonistic calls made by mothers seeking or trying to attract their offspring (whether pup, yearling or two-year-old). I use "female-attraction call" to refer to non-agonistic calls made by pups or juveniles towards females which they appear to be trying to identify as their mother.

Theoretically, non-tonal sounds (barking, snorts, puffing, chuffs) should not be termed vocalizations, since they are not produced by the vocal chords. However, for simplicity and in the context of this thesis, I use the terms "vocalization" and "call" synonymously to refer to all sounds produced by an animal for the apparent purpose of communication.

3.2.2 Behavioural observations

Preliminary observations of vocalizations were conducted *ad libitum* from the cliff-top bench at beach N4 and during tagging activities on beaches N4 and S3. Calls were compared to descriptions of calls documented for other species of *Arctocephalus* (Stirling 1971a; Stirling and Warneke 1971; Miller 1974) and categorized by their acoustic structure (whether tonal or pulsed, etc., see Appendix B).

To verify the context of each call and the situation in which the call was produced, I recorded the number of calls, and their context, made by adult males and females within a specific sampling area (approximately 135 m^2) for one hour periods within daily time windows of 0630-0830, 1130-1330 and 1600-1800 hours. I collected a total of 220 hours of observations at Beach N4 (72 hours in 1994 (Nov 12 - Dec 12) and 148 hours in 1995 (Sept 27 - Dec 11)). The number of adult male and female fur seals was counted at the beginning of each sampling period to enable the calculation of a standardized measure of calling rate (number of calls per individual per hour). This number was a relative measure, since it was not possible to monitor the amount of migration into or out of the sampling area during the observation period. Over the 220 hours of sampling, the number of males within the sampling area at the start of the observations ranged from one to eight (median = three); that of females ranged from eight to 49 (median = 21).

Each call counted was classified first by the sex of the emitting animal, second by structural type, and third by the type of individual to whom it was made. For vocalizations given in rapid succession, such as barking and puffing, each series of vocalizations separated by a distinct period of silence was recorded as one "call". Those calls that were not obviously directed at any particular individual, or that appeared to be directed towards a group of animals, were defined as calls made "to the colony". Calls that could not be classified by structure or recipient (or both) were recorded as "unclassified", as were vocalizations directed towards other species.

3.2.2 Statistical analyses

Observations in the field indicated that mother fur seals' behaviour changed once there were at least 25 pups present. For example, above this threshold, mothers were much less likely to abandon their pups when humans approached the colony (Majluf and Goebel 1992). Thus, the sampling periods were divided *a posteriori* into three intervals, defined by the level of pupping activity on the beach: *No pups*, *Onset* (1-25 pups present) and *Peak* (>25 pups present) (Figure 3-1). In 1994, sampling periods occurred only during the peak period. In 1995, data were collected in all three periods (n = 52 hrs, 33 hrs and 63 hrs, respectively). Since the presence and number of pups necessarily had an effect on female calling, each period in 1995 was analyzed separately, and only data from the peak period of 1995 were compared to the 1994 data.

I conducted a series of likelihood ratio tests to examine the hypothesis that the way adult fur seals use each call type is dependent on the sex/age class of the recipient. For adult males and females, and for each period of the breeding season, I analyzed a matrix of ten call types and six recipient classes (both variables included an additional category of "unclassified" call types or recipients).

Sound spectrograms were prepared using SIGNAL/RTS (Engineering Design, Belmont, Mass.). Calls were sampled at a rate of 30 kHz over the frequency range 0-12 kHz. Spectrograms were calculated from 256-point fast Fourier transforms, with a corresponding frequency bandwidth of 117 Hz. Some calls contained wide-band extraneous noise which extended into frequency ranges higher than the cut-off at 12 kHz; however, noise above this level was not considered a significant contribution to the overall sound of the call because of the effect of masking by background noise from the colony (Renouf 1991; Moore and Schusterman 1987).

3.3 RESULTS

I distinguished eleven call types which may be grouped into four functional classes: investigation, threat, appeasement and affiliative calls. These are summarized in Table 3-1, with alternate terms used in other studies of *Arctocephalus*.

The peak periods in both seasons were similar both in numbers and distribution of calling (Tables 3-2, 3-3). Since the peak period was most relevant to the rest of my study, I present only those data when referring to frequency and distribution of call usage in the following sections, except where noted (data for the periods prior to and during the onset of pupping are summarized in Tables A-3 and A-4). In all periods of the breeding season, the type of call used by adult South American fur seals was dependent on the recipient of the call (Table 3-4). Calls made by young fur seals were not quantified, so the information presented here on call usage by pups and juveniles has been summarized from field notes only.

Calls made to other species were rare, accounting for 0.55% and 0.15% of adult male and female calling, respectively (Table 3-5). For adult males, interspecific calling appeared to be related to defence against sea lions (*Otaria byronia*), while mother fur seals most often threatened approaching turkey vultures (*Cathartes aura*).

3.3.1 Investigative calls

Barking: a series of low energy, rapid exhalations of air through the nose or slightly open mouth. On a spectrogram, barking was represented as a series of pulses of wideband noise, produced at a rate of approximately 4/sec, for periods ranging from one second to several minutes in duration (Figure 3-2a). No tonal components were present.

Context of barking:

Barking was typically used during non-agonistic investigation of other individuals. The vibrissae were erect and oriented forward, and the emitting animal usually inclined or nodded its head towards the recipient (Figure 3-2b). Barking to females represented 40-50% of all calls made by males (Table 3-2). Males typically responded to agonistic interactions among females by approaching the females and barking continously. Males also barked during copulation and in response to other mild disturbances or stimuli such as mothers calling to their pups.

Like males, adult females appeared to use barking in a similar way, although rarely and restricted to other females and juveniles (Table 3-3). Females sometimes barked when an apparently non-threatening individual approached them too closely.

3.3.2 Threat calls

Threat calls were grouped into two series of graded vocalizations: non-tonal or "respiratory" sounds (Peters and Wozencraft 1989), produced by forceful exhalations, and guttural or distinctively pulsed sounds, produced by vibration of the vocal cords.

a) Respiratory threat calls

Puffing: a series of strong exhalations and inhalations produced in rapid succession. Puffing was distinguished from barking by medium to high levels of energy and a tendency towards pulsation and greater complexity of call elements (Figure 3-3a).

Chuff: a high intensity sound of no more than 500 msec, produced by a loud, forceful exhalation from the larynx, often made as the animal threw itself down on its ventral surface. Chuffs were usually produced singly or in very short series and were often immediately followed by sharp inhalations which appeared on a spectrogram as a pulse of lower intensity (Figure 3-3b).

Snort: a single sharp exhalation of air, given with the force of a puff or even a chuff. This sound was comprised of high intensity wide-band noise; no pulsation or tonal components were present (Figure 3-3c).

b) Guttural sounds

Growl: a low energy, rapidly pulsed call with dominant frequencies below 2 kHz, varying in duration from one to five seconds (Figure 3-4a).

Low Intensity Threat Call (LITC): a pulsed call of moderate duration (one to two seconds) and moderate to high energy. It was distinguished from growls by its intensity and by the tendency for wideband noise to overlay the dominant frequencies (Figure 3-4b).

Guttural Threat Call (GTC): a distinctive slowly pulsed, high energy call with no noisy components or tonal structure. Each pulse within the call could be distinguished from the next on spectrograms (Figure 3-4c) and by human ear, to which the calls sounded like a series of "guug-guug-guug".

Full Threat Call (FTC): a high energy call typically composed of two parts: a strongly pulsed, low frequency component which resembled an LITC or a GTC, followed by a higher frequency tonal component with a fundamental frequency of 0.7 - 1.0 kHz. Several harmonics were usually present, and the duration ranged from one to two seconds (Figure 3-4d). FTCs varied in structure among both adult males and females (Figure 3-5).

Context of threat calls:

Threat calls comprised 30-50% of calls made by both males and females, and in both cases the recipient of the call was most often a member of the same sex (Tables 3-2, 3-3). Males used the full range of threat calls when interacting with other males, but mainly threatened females with growls and paid little or no attention to pups and juveniles (Table 3-4). Adult females used growls and puffs most frequently, while most of the higher intensity threat calls were produced rarely (Table 3-3).

Snorts were not included in the analysis of call usage because they were produced infrequently and were difficult to detect. I observed snorts being made by territorial males as an unfamiliar male approached, and on occasion by challenging males as they approached an occupied territory. Of the 34 snorts recorded during the 148 hours dedicated to call quantification in 1995, two were directed to a juvenile sea lion that was approaching the colony, one to a juvenile fur seal and the remainder to adult male fur seals. Neither adult females nor juveniles were observed to produce snorts.

Calls indicating a low to moderate level of aggression, such as growls and puffs, were used most frequently by both adults (Tables 3-2, 3-3) and juveniles, although usage was not quantified for the latter. Adult males also produced LITCs (12-20% of threat calls); however, these were never heard from adult females or juveniles. Growls, LITCs and puffs appeared to form a gradient of aggressive intent. Growls were very low intensity threat calls that were not necessarily directly focused towards any one individual, nor associated with a particular posture. They appeared to be used in response to the slightest perceived threat, including nearby turkey vultures and penguins passing through the colony (Table 3-5). LITCs were typically made with the head and body oriented directly toward the recipient, most often an intruding male, apparently conveying the potential for the level of threat to escalate. Puffing seemed to indicate a moderate level of intensity, and was often accompanied by oblique staring, open-mouth gaping, head shaking and lunging (Figure 3-3d). This was the first level at which physical contact such as biting was seen to follow. Of female threats to other females, almost 20% consisted of puffing, whereas female rarely puffed to males (Table 3-3).

For adults of both sexes, growls, puffs or LITCs also seemed to be effective in intimidating pups or juveniles to vacate a space that they intended to use; indeed, this was the only context in which I observed adult males vocalizing to young fur seals. Growls and puffs were often produced by pups, yearlings and juveniles (two- and three-year-olds). Most of these occurred during play, such as mock territorial disputes or mock fighting. I also saw pups puffing in response to being approached by turkey vultures or humans. Yearlings also growled in response to threatening adult males and females.

High-intensity agonistic calls such as guttural threats, chuffs and full threat calls were typically used during situations of acute aggression, in which the animal seemed prepared to fight (Figure 3-4e). Thus, the calls were infrequent and comprised 10-15% of male threats and less than 1% of female threat calls (Tables 3-2, 3-3). Guttural threat calls were highly agonistic and were not given as casually as growls or LITCs. While making this call, the head was typically oriented directly to the threatening individual, with the neck outstretched in the alert posture (Stirling 1971a). Chuffs occurred rarely, typically in boundary disputes between neighbouring territorial males. Although full threat calls seemed to indicate the highest level of arousal, males produced them twice as often as guttural threats and chuffs (Table 3-2). Full threat calls were made in response to a significant perceived threat, such as during territorial conflicts between males or by both sexes towards humans or adult sea lions (Table 3-5) that approached the colony. FTCs were produced either directly toward the recipient, like guttural threat calls, or with the neck stretched and nose pointed upwards, staring obliquely at the opponent. Both of these postures accentuated the size of the emitting animal and probably enhanced the effect of the display.

Males also made infrequent full threat calls "to the colony", possibly advertising their status to nearby males or females (Table 3-2). I typically observed this behaviour in adult males that had just won a territorial dispute and ousted the previous male. One male produced over 80 full threat calls during the first 20 minutes after gaining a new territory (this did not occur during observation periods dedicated to quantification of call usage, and therefore is not represented in Table 3-2). The male did not orient to any other animal in particular and could not see any neighbouring territorial males because of a high rock. When given in this context, full threat calls appeared to be contagious, and neighbouring males often began to call also. Territorial males also produced full threat calls spontaneously when a fight occurred in an adjacent territory.

3.3.3 Appeasement calls

Submissive Call: a high-pitched, strongly frequency-modulated call, ranging in duration from one to five seconds (Figure 3-6a). This was a high intensity call and was often repeated once or twice.

Context of submissive calls:

Submissive calls were not emitted frequently by either females or males, although females produced them more often (3-4% vs. 0.1-0.2% of all vocalizations), and the majority were given between females (Tables 3-2, 3-3). The calls were given by subordinate animals after an agonistic encounter and were usually accompanied by the open-mouth display or submissive posturing such as facing away (Figure 3-6b). Smaller or apparently younger females used the submissive call when threatened by neighbouring females. I also observed females using the submissive call continuously as they attempted to move from one side of the colony to the other, particularly when moving to the tidal area in the morning.

3.3.4 Affiliative calls

Pup-Attraction Calls (PACs): females typically made high energy calls of moderate to long duration when calling to their pups. The structure of the calls tended to be complex and was typically composed of an initial pulsed component, followed by a high-pitched tonal component (fundamental frequency 0.7 - 1.0 kHz) that ended abruptly with a rapid decrease in frequency (Figure 3-7a). However, as noted by Trillmich and Majluf (1981), PACs appeared to be highly individualistic; some females produced a pure, monotonic call with flat, parallel harmonics (Figure 3-7b), while others had virtually no tonal components within their calls (Figure 3-7c).

Female-Attraction Calls (FACs): these calls also varied substantially between individuals, but like pup-attraction calls, were typically pulsed at the start and ended with tonal elements that were sometimes strongly frequency-modulated (Figure 3-7d). Most FACs were high energy and high-pitched, with a fundamental frequency of 1.0 - 1.5 kHz. Yearlings and juveniles (up to three years of age) that were not yet weaned also produced a loud, high-pitched pulsed call with strong frequency modulation (Figure 3-7e).

See Chapter 6 for quantification and discussion of individual variation of pup-attraction calls and female-attraction calls of pups. See Chapter 7 for comparisons of PACs and FACs produced by mother-pup pairs and a discussion on heritability of call structure.

Context of affiliative calls:

Pup-attraction calls were given almost exclusively to pups or juveniles, and were the most common call used by females during the peak of the pupping period (Table 3-3). On nine occasions, I observed adult territorial males producing a call identical to the pulsed pup-attraction call, although the context was unknown (Table 3-2). Adult males were never heard to produce purely tonal calls such as that illustrated in Figure 3-7b or those described by Pierson (1987: Fig. 4a).

Pup-attraction calls were produced in all circumstances in which mothers may call to their offspring, ranging from searching for their pups after returning from an offshore foraging trip (Figure 3-7f), to reuniting after being separated for minutes or hours on the beach, to lying in physical contact with their pups. Females also gave pup-attraction calls to the colony in general, especially in the day or so immediately prior to parturition. I also observed mothers making these calls continuously during parturition (Table 3-6). Mother-pup reunion behaviour is described in more detail in Chapter 5.

Pups up to about a week old appeared to give female-attraction calls indiscriminately to any passing female. After this, however, pups called primarily to their own mothers, either spontaneously or in response to their mother's PAC. Yearlings that had not yet weaned continued to produce FACs, particularly while searching for their mothers within the colony. Calls of both pups and yearlings were frequently accompanied by vigorous head shaking, particularly when their mother was returning from sea.

Vocal bouts between mothers and pups often occurred when the pair was resting, particularly in the early morning. These bouts were usually initiated by the female, who would give several low-energy calls to her pup. If the pup awoke, it often vocalized in response. The pair then called back and forth for up to a minute, at a rate of about 1-2 calls per second each, and nursing often followed. This type of restive calling may serve to reinforce the bond between the mother and the pup and enable them to learn each other's call (see Chapter 7).

In addition to resting bouts, a mother typically called to her pup when it left her side. She sometimes raised herself up on her foreflippers to call, usually increasing the energy of the call as the pup moved away. The pup often remained where it was and called back to its mother. At this point, she either went and retrieved the pup to where she had been sitting, or called once or twice more before going back to sleep, leaving the pup to sleep where it was or to wander off and play. To incite the pup to follow or remain close, mothers also called to their pups during their daily thermoregulatory movements up or down the beach. If pups did not follow, mothers sometimes carried them through the colony by their neck, which invariably resulted in loud, frequency-modulated versions of pups' calls.

The distance of separation between mother and pup appeared to have an effect on the rate of calling. For two tagged mother-pup pairs observed in 1994, mothers called more when the pair was separated by more than three female body-lengths, while pups called more when the pair was in close contact (Figure 3-8). These data suggest that for females, the main function of calling may be to initiate contact by decreasing the distance between them and the pup, while pups that vocalize while in close contact with their mothers might be attempting to initiate suckling.

3.4 DISCUSSION

At Punta San Juan, both male and female South American fur seals produce a large range of vocalizations. In this section, I explore the relationship between form and function of the various types of calls, and compare these to descriptions of vocal behaviour in other species of *Arctocephalus* (Table 3-7).

3.4.1 Barking and threat calls: graded signals?

Barking occurs in all otariids (see review in Miller 1991: 209-211). In most species, barks are tonal sounds; interspecific variation occurs in amplitude, duration and frequency characteristics. In sea lions and South African / Australian fur seals (*Arctocephalus pusillus*), barking is produced with the mouth open, resulting in a loud, long "honking" vocalization (Rand 1967), while other Arctocephaline fur seals bark with the mouth nearly or completely closed, sounding like a soft, high-pitched "whimper" (Table 3-1; compare spectrograms in Peterson *et al.* 1968 (Fig. 3); Peterson and Bartholomew 1969 (Figs 1,2); Stirling and Warneke 1971 (Fig. 4); Pierson 1987 (Fig. 5a)). In contrast, barking in the South American fur seal is a very brief, soft call with no harmonic structure, most similar to those described for the northern fur seal, *Callorhinus ursinus* (Lisitsyna 1973: Fig. 2-III). This likely explains why Trillmich and Majluf (1981: 319) were unable to detect "anything remotely resembling the barking of a sea lion (*Zalophus californianus*) or a South African fur seal (*A. pusillus*)".

Although the barking of South American fur seals differs structurally to varying degrees from that of other fur seal species, the call appears to have the same investigative function. Adult males used it primarily towards adult females, especially while investigating sexual receptivity. Both adult males and females also appeared to use barking towards subordinate animals, perhaps to affirm their status or location as suggested by Stirling and Warneke (1971). Similar repetitive sounds have been reported for other mammalian species and may have evolved as "an acoustic consequence of more active olfactory exploration" (Gould 1983: 305)

Snorts are subtle, difficult to detect and, not surprisingly, have only infrequently been reported in the literature (Table 3-7). Snorts appeared to be intermediate between barking and puffing in both acoustic structure and apparent function. In South American fur seals, I found that snorts (and perhaps barking, when used between females) were used not only to signal that more information was required about the recipient of the calls, but also to indicate that there was a potential for increasing hostility. This is consistent with Winn and Schneider's (1977: 831) observation that among pinnipeds, snorts may have "universal significance in low-intensity warning".

I suggest that the threat vocalizations used by South American fur seals form two graded series of sounds, which for convenience I have termed respiratory calls and guttural calls. Respiratory calls are audible, noisy exhalations (sometimes followed by inhalations) which appear to form a continuum of harsh, non-tonal sounds ranging from soft, low-energy barking to loud, high energy chuffs. I include barking in this category because structurally it appears to be a soft, low energy version of the puff (compare Figures 3-2a, 3-3a); however, inhalation sounds are not usually apparent during barking. Morton (1977) proposed that as sounds become louder and more harsh, the message of the signal indicates higher levels of hostility. In this study, the non-tonal sounds made by South American fur seals became louder and more forceful as calls intergraded from barking to snorting to puffing to chuffing, and the behaviours associated with them indicated increasing intensity of aggression and potential for physical contact. Similarly, the guttural calls could also be thought of as a series of intergrading sounds which are based on the low frequency, pulsed structure of a growl (Figure 3-4). As the relative levels of energy, rate of pulsation and loudness of these calls increased, the level of hostility appeared to rise.

It seems reasonable that calls used in agonistic situations would show gradation of structure and form. Since aggressive encounters typically occur face-to-face or over short distances, graded vocalizations would allow for fighting and display behaviour to be more flexible, and animals would be more likely to make use of the context of the situation to supplement the behavioural message in the call (Smith 1977; Morton 1982; Miller 1991). For South American fur seals, context may include the age, physical condition and experience of the receiver of the call. If adult males are able to recognize one another, as suggested by Stirling (1971a), Stirling and Warneke (1971), and Roux and Jouventin (1987), the identity of the sender would provide important information to the receiver, particularly if the receiver has had previous experience interacting with the sender. The importance of visual displays (such as facial expression, body posture and movement) concurrent with vocal displays cannot be overlooked in these interactions (Miller 1975, 1991). For example, by making himself look bigger, a male may be able to convey a high intensity threat with lower energy vocalizations. Also, subordinates may reduce the risk of injury by adjusting their threat vocalizations and posture in response to the behaviour of dominant animals.

3.4.2 Submissive calls

In contrast with the graded threat calls, discrete signals are believed to indicate an evolutionary premium on lack of ambiguity (Altmann 1967). For example, in situations of appeasement and escape, it is critical for the retreating animal to make its message clear and thereby avoid further conflict and injury. Submissive calls of South American fur seals showed little variation; the calls were typically loud, long, high-pitched and directional, which would allow the sender to be readily located (Marler 1955). From examination of the literature (Tables 3-1, 3-7), submissive calls among species of *Arctocephalus* appear similar in acoustic structure and associated visual cues (see Stirling 1971a (Fig. 5c); Miller 1975). These results support Andersson's (1980) proposal that submissive calls would be expected to be phylogenetically stable because of the potentially disastrous consequences to the sender of the signal if the meaning was misinterpreted.

Submissive calls of South American fur seals were somewhat similar in structure to FACs used by yearlings and two-year-olds; both had the same loud, high-pitched, frequency-modulated sound (compare Figures 3-6a, 3-7e). Juvenile animals would be expected to produce higher-pitched calls than adults because of physical limitations of size and musculature of the vocal tract. However, the resemblance of submissive or appeasing calls with calls of juveniles has also been reported in other mammals (e.g. Green 1975; Conner and Whitworth 1985). Morton (1977) suggested that submissive calls may have evolved as a vocal indication of small size, which might cause the receiver to recognize that the perceived threat is lower and reduce its level of hostility accordingly. Similar strategies appear to have evolved in mountain sheep, in which subordinate rams mimic the behaviour of estrous ewes to avoid being attacked by dominant rams, while anestrous ewes mimic juvenile behaviour to reduce unwanted attention by rams (Geist 1971).

Alternatively, in the South American fur seal, juvenile calls may resemble submissive calls simply to reduce attention from adult males. At Punta San Juan, submissive calls seem to cause dominant animals to reduce hostility or even ignore the senders (consider the continuous use of these calls by subordinate females attempting to pass through the colony). Juvenile fur seals remaining on the breeding colony are typically not yet weaned or have been weaned recently (Majluf 1987), and still maintain vocal contact with their mothers. If their calls resemble submissive calls, juveniles might therefore experience a reduced risk of agonistic or sexual interactions from territorial males.

3.4.3 Acoustically complex calls

Full threat calls and affiliative calls are also used in situations in which the message conveyed by the call needs to be unmistakeable. In the South American fur seal, full threat calls indicate high levels of aggression and readiness to fight. Pup-attraction calls are only used by mothers toward their young, whether to reunite or to maintain contact with the pup on the colony. Similarly, although pups are capable of producing a range of sounds including puffs and growls, their high-pitched female-attraction calls are primarily used toward those females which they recognize as their mother. Other studies on *Arctocephalus* have postulated the same functions for these calls (Stirling 1971a; Stirling and Warneke 1971; Miller 1975; Trillmich 1981; Pierson 1987; Roux and Jouventin 1987; Miller 1991).

Although used in different circumstances, these three calls have several characteristics in common. They are all acoustically complex, typically consisting of both pulsed and tonal components (compare Figures 3-5, 3-7). Unlike other threat vocalizations and barking, they are typically loud, long calls and may be used over long distances as well as in close contact. Finally, all three seem to have an important role in individual recognition (Chapter 6). The variable structure of FTCs among adult males and females suggests that individuality of these calls would be possible (Figure 3-5). Although I have not yet quantified individuality of FTCs made by South American fur seals at Punta San Juan, my field assistants and I were able to distinguish several adult males by their FTC.

The structural similarity of full threat calls and affiliative calls is likely related to the function of the calls. Calls used over long distances, without the benefit of other sensory and contextual cues, are typically of a discrete form to reduce ambiguity (Marler 1976; Morton 1977, 1982; Miller 1991). Furthermore, high frequency sounds with harmonic structure attenuate less rapidly over long distances and tend to be directional, so are more common in sounds used to attract the attention of the recipient or aid in the location or detection of the sender (Marler 1955; Green and Marler 1979). Also, complex calls allow large variation in both acoustic characteristics and syntactical organization, which would enable identity information to be encoded (Beecher 1989; Miller and Murray 1995).

The FTC of South American fur seals is comparable to those illustrated for other species of *Arctocephalus* (Stirling 1971a (Fig. 5a,b); Stirling and Warneke 1971 (Fig. 5d); Pierson 1987 (Fig. 4); Roux and Jouventin 1987 (Fig. 5); see also Tables 3-1, 3-7). The underlying compound form of the calls is apparent in most of the published spectrograms, even though all of the species studied seem to exhibit individual variation.

Roux and Jouventin (1987) suggested that compound FTCs (containing high-pitched tonal components) are only given by species that inhabit rugged terrain that limits the use of visual or olfactory cues for recognition among territorial males. In contrast, they hypothesize that species which breed in more open habitat, such as the Galapagos (*A. galapagoensis*), Antarctic (*A. gazella*), and South African fur seals, would have less use for FTCs. Whether such a trend exists is uncertain. The FTCs of Antarctic fur seals do not appear to contain tonal components (Stirling and Warneke 1971). According to Stirling and Warneke (1971) and Miller (1991), South African fur seals do not produce FTCs at all, but Rand (1967: 20) described a "deep-throated roar" and Caudron (1991) a "*rugissement*" (roar) produced by an adult male (although she stated that the context of this sound was difficult to determine in the captive situation of her study). There are no published descriptions of calls made by male Galapagos fur seals.

All fur seal females and pups produce affiliative calls (Table 3-7), and those of South American fur seals differ little in overall structure from those of other species of *Arctocephalus*. Harmonic structure appears to dominate the PACs of most fur seals, although pulsation at the start of the calls is not uncommon (Stirling and Warneke 1971 (Fig. 1); Trillmich 1981 (Figs 2,4); Pierson 1987 (Fig. 8a); Roux and Jouventin 1987

(Fig. 5)). In all species, pup calls are typically high-pitched and complex, as illustrated by the variety of onomatopoetic terms found in the literature (e.g. bleat, wail, bawl, staccato call, whimper, baa; sources as for Table 3-7). Calls of South American fur seal pups were similar to those illustrated for other species (Stirling and Warneke 1971 (Fig. 2); Trillmich 1981 (Fig. 5); Pierson 1987 (Fig. 8b); Roux and Jouventin 1987 (Fig. 6a). Individual variation of affiliative calls is explored in more detail in Chapter 6.

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Table 3-1. Call names used in this study and alternate names used in the literature for *Arctocephalus* spp.

Vocalization [a]	Alternate names [b]
Investigation	
Bark	whimpering (1,2,6,7,8,14), speaking (9), honking or grunting or clucking (12), whickering (10,13), whicker-bark (11), *aboiement* (3,18), *resonancia nasal* (21)
Threat	
Snort	oral snorting (7), *renâcler* (3)
Puffs	coughing (4,9,10,12), hissing (12), *menace toussée* (3)
Chuff	boundary puff (11)
Growl	low-intensity threat (7,11), *grondement / grognement sonore* (3), *gruñido* (22)
Low intensity threat (LITC)	low roar (9), short roar (17), low threat call (20), *menace de faible intensité* (18), *rugido bajo* (21), *rugido grave* (22)
Guttural threat call (GTC)	choke (15,9?), guttural challenge (16,17), high intensity guttural threat (17), *provocation gutturale* (18), *vocalisation gutturale saccadée* (3)
Full threat call (FTC)	roar (4,9,10,12), trumpeted roar (6,7), territorial call (13), *menace de forte intensité* (18), *rugissement* (3)
Appeasement	
Submissive call	howl (9), whine (15), *cri de soumission* (18), *alarido* (21,22)
Affiliation	
Pup-attraction call (PAC)	bleat (9), bellow or lowing (12), bawl (10), pup-contact call (19), *cri d'appel du jeune* (18), *cri de la mère* (3), *balido* (22)
Female-attraction call (FAC)	bleating (2,9,12), tantrum call (5), *cri d'appel de la mère* (18), *cri du petit* (3), *balido* (22)

[a] Calls arranged in presumptive functional classes.

[b] Sources: (1) Bonner 1958; (2) Bonner 1968; (3) Caudron 1991; (4) Feldman 1993; (5) Majluf 1987; (6) Miller 1971; (7) Miller 1974; (8) Miller 1975; (9) Paulian 1964; (10) Peterson *et al.* 1968; (11) Pierson 1987; (12) Rand 1967; (13) Roux and Jouventin 1987; (14) Shaughnessy *et al.* 1988; (15) Stirling 1970; (16) Stirling 1971a; (17) Stirling and Warneke 1971; (18) Tollu 1982; (19) Trillmich 1981; (20) Trillmich and Majluf 1981; (21) Vaz Ferreira 1956; (22) Vaz Ferreira 1971.

Table 3-2. Distribution (%) of calls made by adult male fur seals during the peak pupping periods of the 1994 and 1995 seasons. (n = number of sampling periods; N = number of calls observed in each category, pooled across all sampling periods). Values of .0 indicate proportions < 0.05%.

a) 1994 (n = 72)

	Recipient of call						
Call type	Female	Male	Pup	Juv.	Colony	Unclass.	N
Barking	39.0	3.6	–	.2	1.4	5.1	884
Threat calls (total)	8.4	34.6	–	–	.5	4.7	864
Puffing	2.0	6.6	–	–	–	.2	157
Chuff	–	1.7	–	–	–	.1	32
Growl	6.1	11.8	–	–	.1	1.3	346
LITC	.2	9.0	–	–	.3	2.0	206
Guttural threat call	.1	1.9	–	–	–	.5	44
Full threat call	–	3.6	–	–	.1	.7	79
Submissive calls	–	.1	–	–	–	–	2
Affiliative calls	–	.1	–	–	.3	.1	9
Unclassified	.3	.2	–	–	.4	1.8	37
N	857	692	0	3	46	198	1796

b) 1995 (n = 63)

	Recipient of call						
Call type	Female	Male	Pup	Juv.	Colony	Unclass.	N
Barking	53.4	2.5	.2	.5	.3	1.9	1548
Threat calls (total)	7.5	27.9	.2	.4	.2	2.7	1021
Puffing	1.3	2.8	–	–	–	.2	112
Chuff	–	1.0	–	–	–	–	25
Growl	6.1	16.4	.2	.2	.0	1.1	633
LITC	.1	4.5	–	.2	.2	.6	146
Guttural threat call	–	.2	–	–	–	.1	6
Full threat call	–	3.0	–	–	–	.7	99
Submissive calls	.0	.2	–	–	–	–	5
Affiliative calls	–	–	–	–	–	–	0
Unclassified	.7	1.2	–	.0	.0	.2	57
N	1620	834	11	23	16	127	2631

Table 3-3. Distribution (%) of calls made by adult female fur seals during the peak pupping periods of the 1994 and 1995 seasons. (n = number of sampling periods; N = number of calls observed in each category, pooled across all sampling periods). Values of .0 indicate proportions < 0.05%.

a) 1994 (n = 72)

	Recipient of call						
Call type	Female	Male	Pup	Juv.	Colony	Unclass.	N
Barking	–	–	.0	–	–	.1	12
Threat calls (total)	19.4	5.8	.6	.5	.0	4.3	5519
Puffing	5.2	.3	.0	.0	–	.2	1047
Chuff	–	–	–	–	–	–	0
Growl	14.1	5.5	.6	.5	.0	4.0	4445
LITC	–	–	–	–	–	–	0
Guttural threat call	.1	.0	.0	.0	–	.0	26
Full threat call	–	.0	–	–	–	–	1
Submissive calls	2.7	.1	–	–	–	.0	518
Affiliative calls	.2	.1	59.0	.4	.7	5.0	11405
Unclassified	.1	.1	.1	.0	–	.9	224
N	4030	1108	10762	161	130	1840	18031

b) 1995 (n = 63)

	Recipient of call						
Call type	Female	Male	Pup	Juv.	Colony	Unclass.	N
Barking	.4	–	.0	.0	–	.1	80
Threat calls (total)	25.5	10.7	1.2	1.2	–	.9	6700
Puffing	7.4	.4	.1	.0	–	.1	1358
Chuff	.0	–	–	–	–	–	1
Growl	18.0	10.2	1.2	1.2	–	.8	5332
LITC	–	–	–	–	–	–	0
Guttural threat call	.0	.0	–	–	–	.0	9
Full threat call	–	–	–	–	–	–	0
Submissive calls	3.5	.4	–	–	–	.0	670
Affiliative calls	–	.1	55.4	.3	–	.1	9375
Unclassified	.2	.0	.1	.0	–	.1	55
N	5030	1888	9646	253	0	193	17010

Table 3-4. Likelihood ratio tests of independence between the type of call used by adult South American fur seals and the recipient of the call, for each period of the pupping season in 1994 and 1995. All tests are significant at $p < 0.001$.

	Adult males		Adult females	
Period of season [a]	G^2	df	G^2	df
94: Peak	1222	36	19850	35
95: No pups	785	32	2253	28
95: Onset	755	35	4136	30
95: Peak	1791	40	21860	28

[a] As for Figure 3-1; see text for explanation.

Table 3-5. Summary of vocalizations directed towards other species by South American fur seals, during the call observation periods of both years (n = 220 hrs).

a) Adult males (34 of 6202 calls recorded)

	Type of call							
Species[a]	Bark	Growl	LITC	Puff	GTC	FTC	Snort	Total
Sea lions								
Adults	5	5	9	3	1	6	--	29
Juveniles	--	--	1	--	--	--	2	3
Vultures	1	--	--	--	--	--	--	1
Crab	--	1	--	--	--	--	--	1

b) Adult females (66 of 44538 calls recorded)

	Type of call			
Species[a]	Growl	Puff	Unclass.	Total
Sea lions				
Adults	3	5	2	10
Juveniles	5	--	--	5
Vultures	36	3	1	40
Gulls	2	--	--	2
Penguins	7	1	--	8
Crab	1	--	--	1

[a] South American sea lion (*Otaria byronia*)
Turkey vulture (*Cathartes aura*)
Peruvian gull (*Larus belcheri*)
Humboldt penguin (*Spheniscus humboldti*)
Crab (unidentified)

Table 3-6. Vocal behaviour of South American fur seal mothers and pups at parturition, arranged by the first of the pair to call, and in ascending order of the time taken for the mother to call. From 1995 field notes at beach N4.

				Time of first call (min)		
Date	# calls in labour	Birth position	First to call	Mother	Pup	Comments
26 Nov	many	breach	pup	0:03	0:02	Mother called continuously after birth
22 Nov	some	head	pup	0:14	1:12	
8 Nov	11	breach	pup	0:27	0:14	
19 Nov	0	breach	pup	0:29	0:25	
19 Nov	0	breach	pup	3:15	0:25	
2 Dec	0	head	pup	4:02	3:12	
25 Nov	0	breach	pup	5:24	4:00	Mother is XX64
26 Nov	0	breach	pup	13:00	0:10	Mother barely called during first 30 min after birth
4 Dec	0	head	pup	13:54	0:27	
2 Dec	many	breach	mother	0:04	1:04	
14 Nov.	0	breach	mother	0:27	0:32	
28 Nov	0	breach	mother	0:31	0:51	
9 Nov	0	breach	mother	0:51	1:26	
24 Nov	some	breach	both	0:53	0:53	Mother is XX52

Table 3-7. Summary of studies[a] that refer to vocalizations made by *Arctocephalus* spp. (excluding this study). Note that the absence of a vocalization in the literature does not rule out the possibility that the vocalization occurs in the species. Latin names are provided in Chapter 1.

Vocalization	S. American fur seal	New Zealand fur seal	Galapagos fur seal	Antarctic fur seal	Juan Fernández fur seal	S. African fur seal	Australian fur seal	Guadalupe fur seal	Subantarctic fur seal
Bark	25	4,9,10,11,20,22		1,2,22	12?[b]	3,16	22	5,6,14,15	13,17,18
Snort		9,10,19				3,16			
Puffs	24					3,16		5,6,14	13
Chuff								15	
Growl	24,26	9,10,18		1,2	12	3,16		5,6,15	13,18
Low intensity threat	24,26	4,19,20,22		22				22	13
Guttural threat	25	4,9,19,20,22		22		3,16	22	22	22
Full threat	24	4,10,20,22		22		3,16		5,14,15	13,17
Submissive call	24,25,26	4,11,20,22	24			16	22	22	13
Pup-attraction call	7,24,25,26	4,8,18,20,21,22	23	2,18,22		3,16	22	6,14,15	13,17,18
Female-attraction call	7,24,25,26	4,8,20,22	23	2,22		3,16	22	6,15	13,17
Others:[c]									
Yelp	26					3,16		5	
Female threat call		4,20,21							
Moan		4,20			12	16			

[a] Sources: (1) Bonner 1958; (2) Bonner 1968; (3) Caudron 1991; (4) Crawley and Wilson 1976; (5) Feldman 1993; (6) Fleischer 1978; (7) Majluf 1987; (8) McNab and Crawley 1975; (9) Miller 1971; (10) Miller 1974; (11) Miller 1975; (12) Norris and Watkins 1971; (13) Paulian 1964; (14) Peterson *et al.* 1968; (15) Pierson 1987; (16) Rand 1967; (17) Roux and Jouventin 1987; (18) Shaughnessy *et al.* 1988; (19) Stirling 1970; (20) Stirling 1971a; (21) Stirling 1971b; (22) Stirling and Warneke 1971; (23) Trillmich 1981; (24) Trillmich and Majluf 1981; (25) Vaz Ferreira 1956; (26) Vaz Ferreira 1971.

[b] Sounds recorded underwater

[c] Vocalizations that were not detected in this study

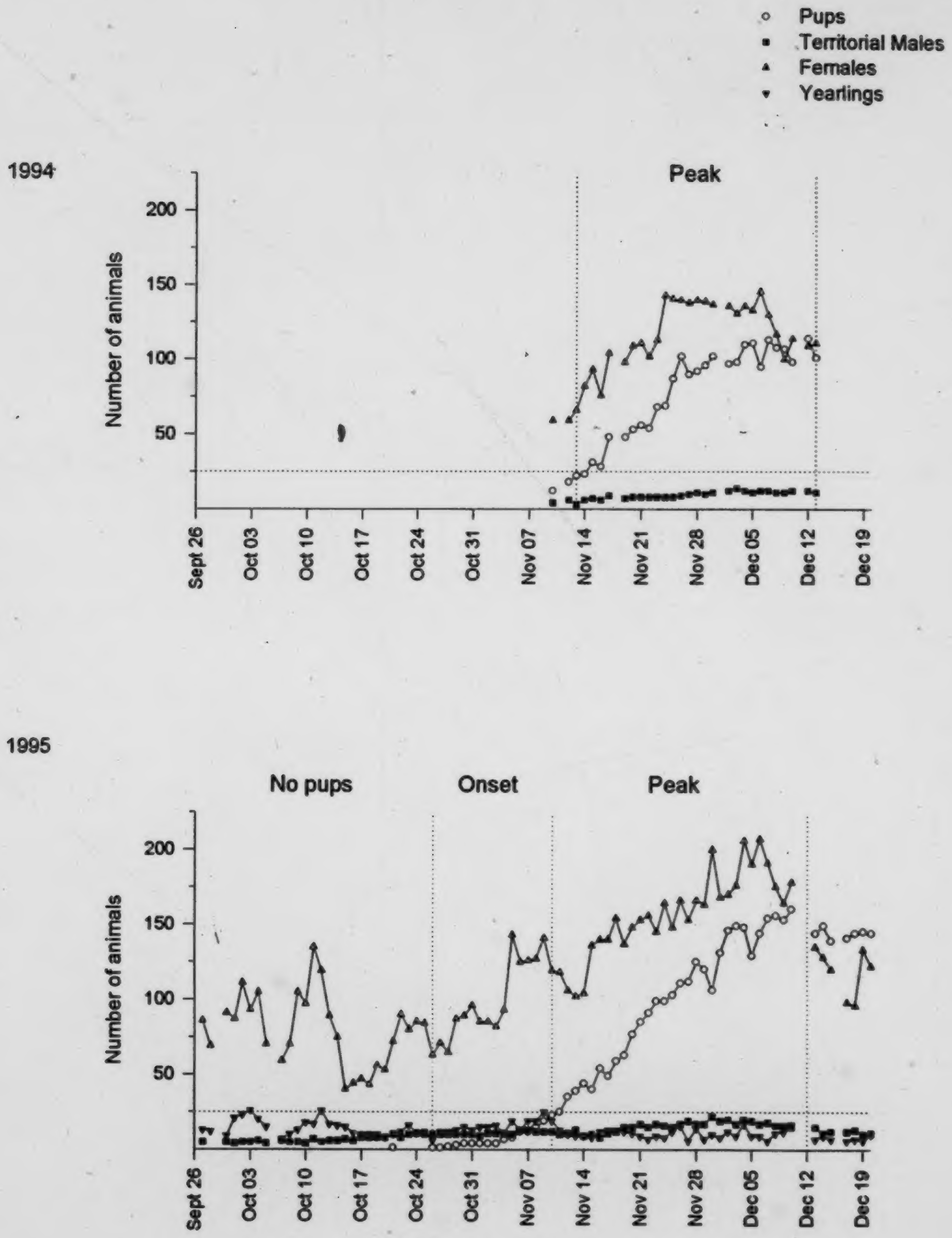

Figure 3-1. Daily census of fur seals at beach N4 in 1994 and 1995. Periods of call usage observations are indicated by the vertical lines.

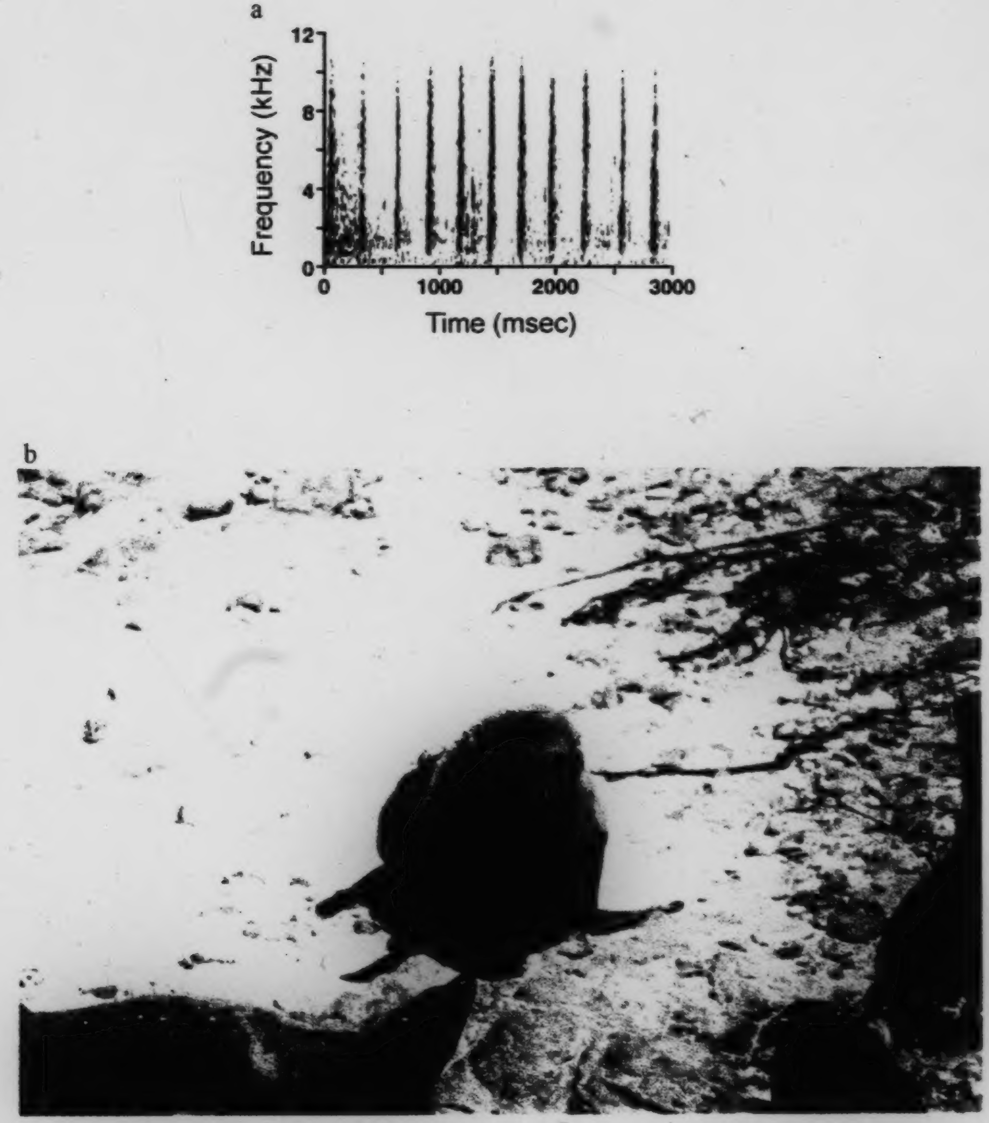

Figure 3-2. Barking by male fur seals. a) Spectrogram of barking (frequency bandwidth = 117 kHz). b) Adult male barking to adult females; note orientation of head and vibrissae.

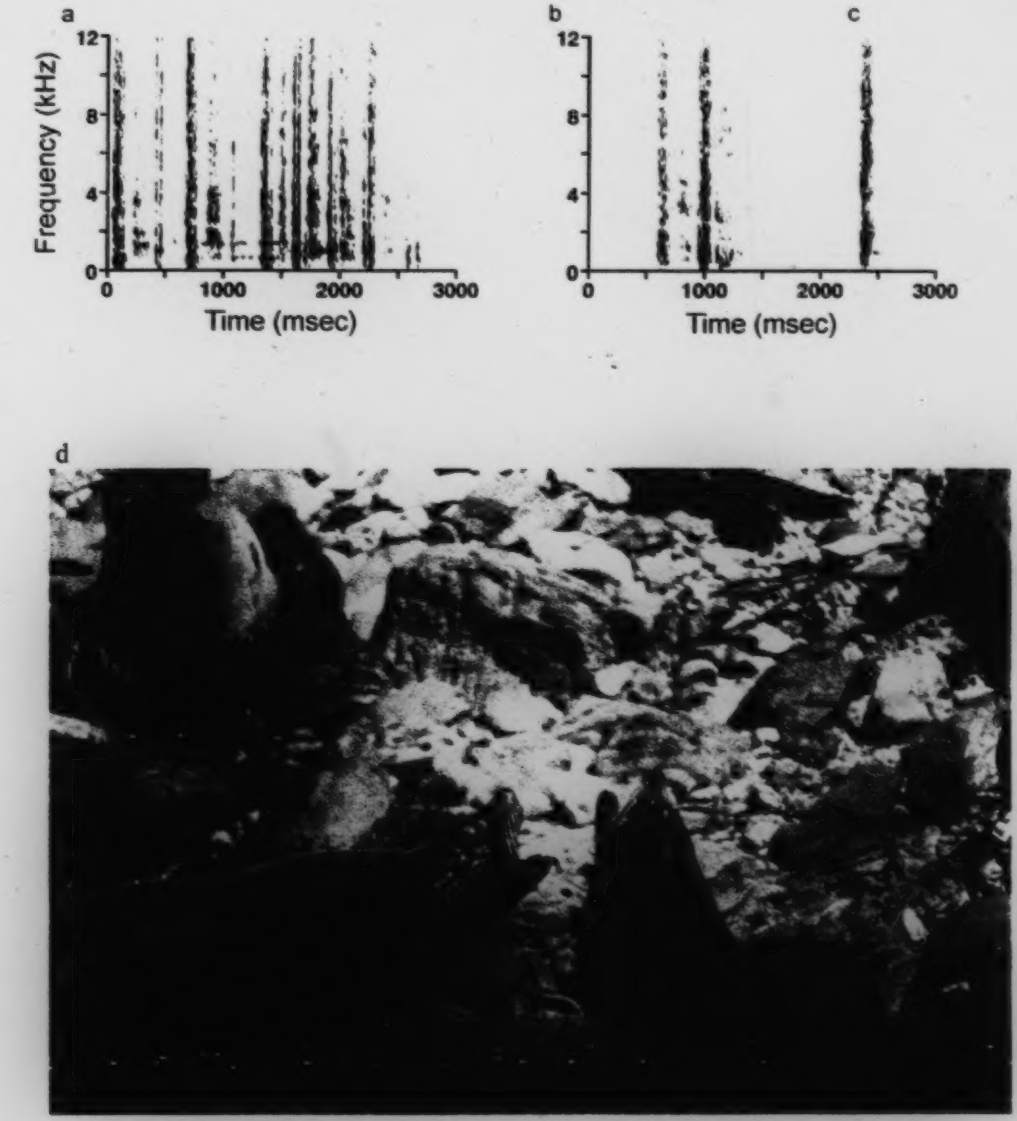

Figure 3-3. Non-tonal threats used by adult fur seals. a-c) Spectrograms of a) puffing; b) two chuffs; c) snort. d) Adult female (at left) puffing to adult female; note use of oblique staring. Frequency bandwidth of spectrograms: 117 Hz.

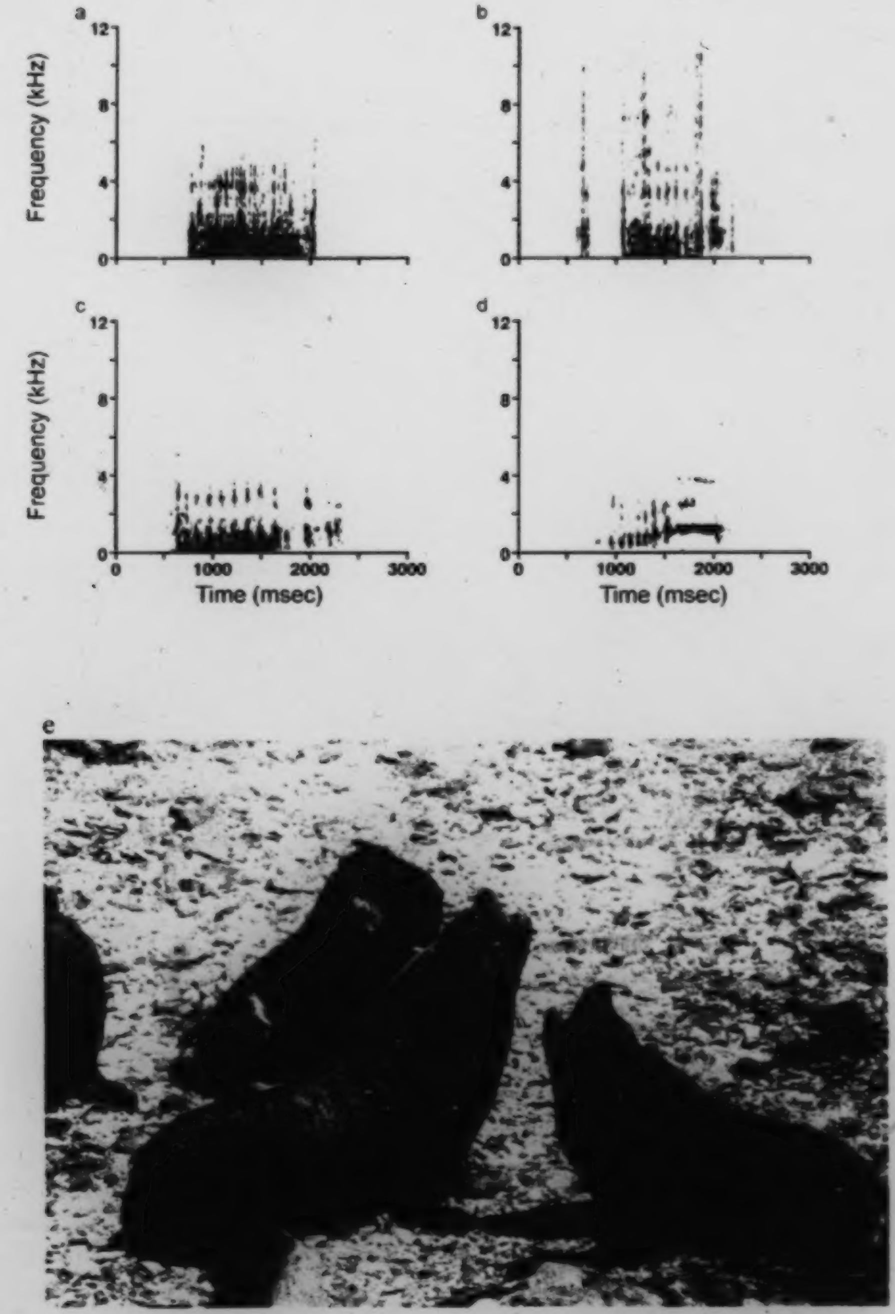

Figure 3-4. Guttural threat calls used by adult fur seals. a-d) Spectrograms of a) growl; b) LITC; c) GTC; d) FTC. e) Adult males exchanging GTCs during a territorial dispute. Frequency bandwidth of spectrograms = 117 Hz.

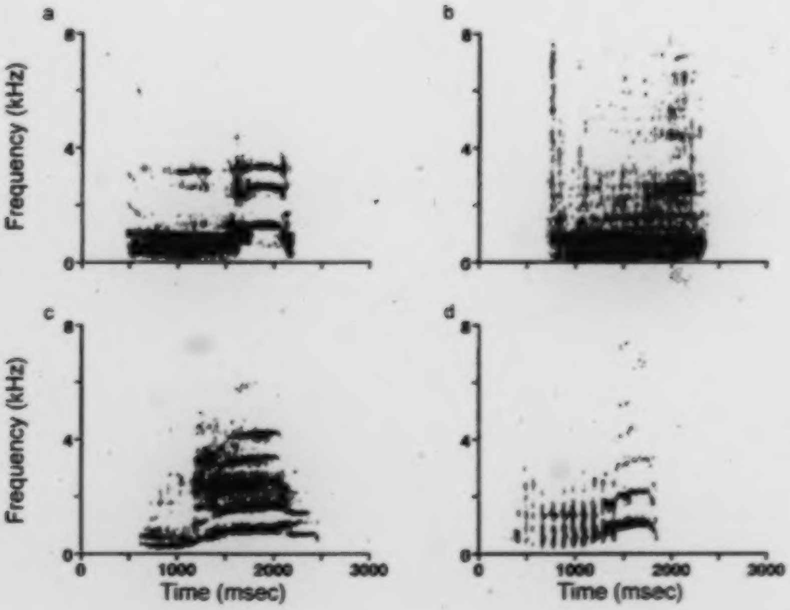

Figure 3-5. Individual variation in full threat calls given by four adult fur seals. a-c) Territorial males; d) Adult female (FTC produced to human). Frequency bandwidth of spectrograms = 39 Hz.

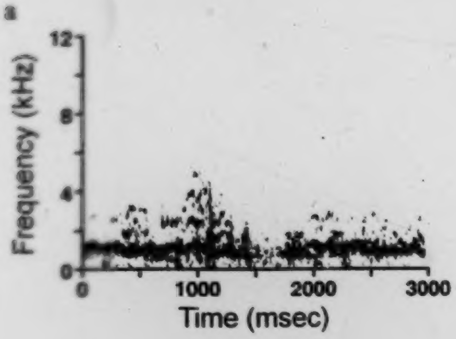

Figure 3-6. Submissive calling by adult fur seals. a) Spectrogram of submissive calls made by retreating adult male after losing a fight with a territorial male. b) Adult female (right) giving submissive call while backing away from adult male (left). Frequency bandwidth of spectrogram = 117 Hz.

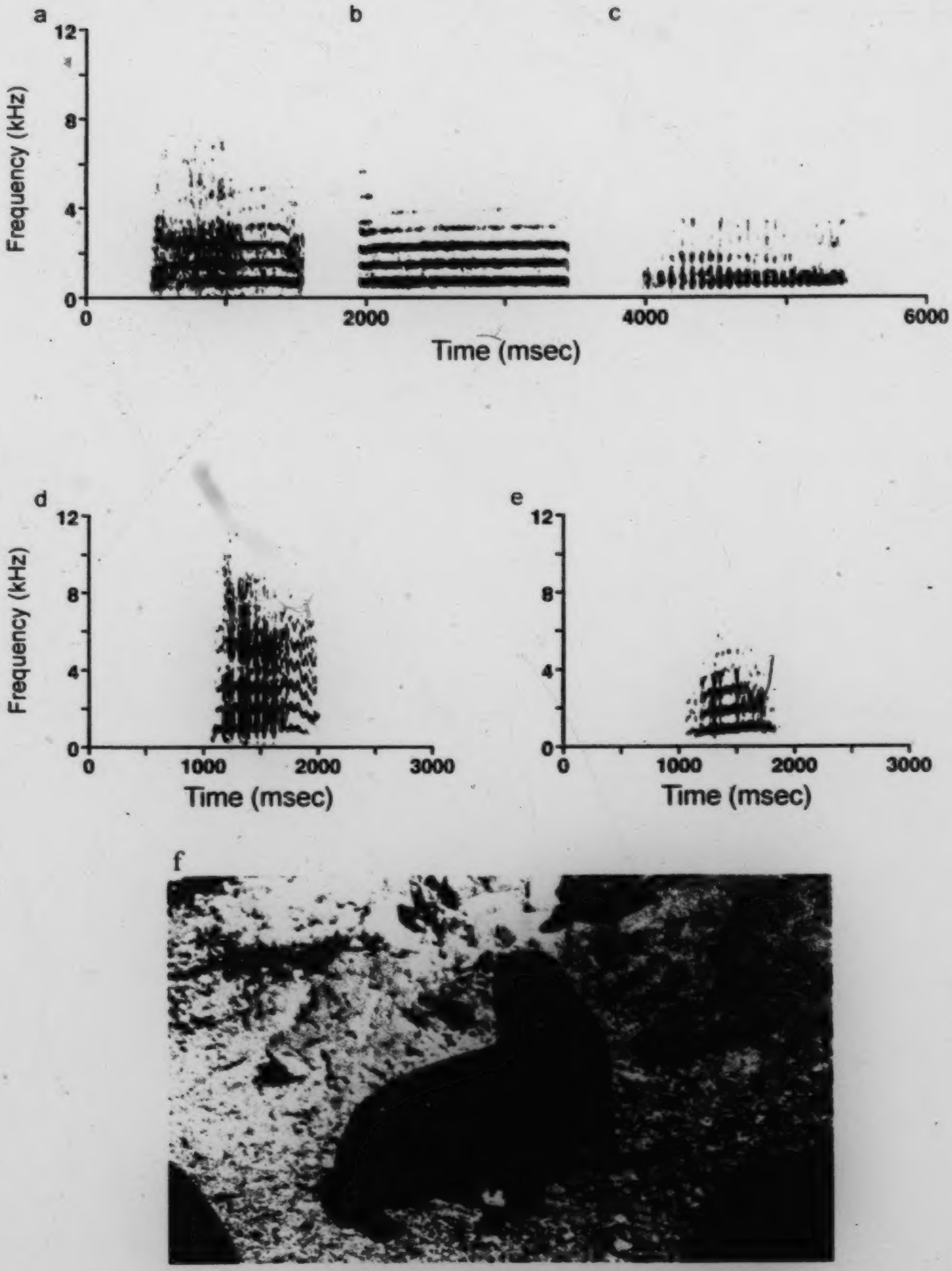

Figure 3-7. Affiliative calling between mothers and their young. a-c) Spectrograms of pup-attraction calls made by three different mothers; d) Female-attraction call made by pup; e) Female-attraction call made by yearling. f) Mother calling to pup; note body raised high on foreflippers; mouth wide open. Frequency bandwidth of spectrograms = 117 Hz.

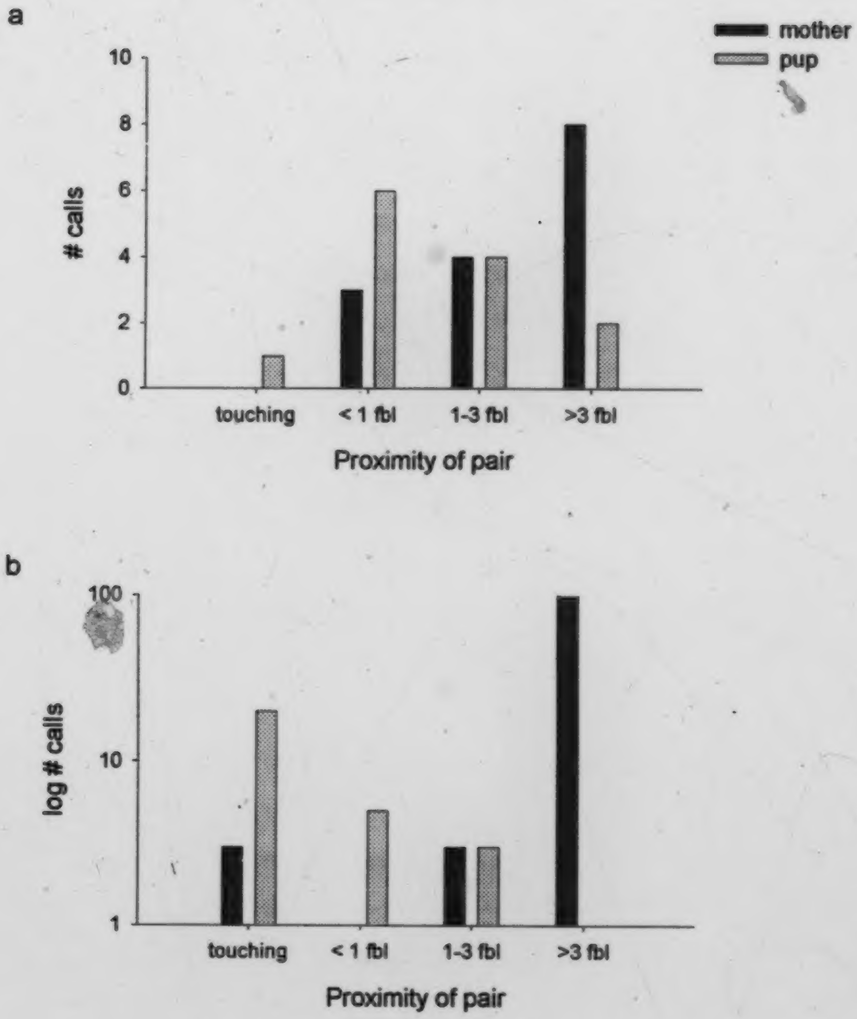

Figure 3-8. Effect of proximity (fbl = female body-length) on calling behaviour of two mother-pup pairs. Note log scale in b).
a) XX80 / XX27 (40 min); b) XX68 / XX63 (60 min).

4. POTENTIAL INFLUENCES ON MATERNAL AGGRESSION IN SOUTH AMERICAN FUR SEALS AT PUNTA SAN JUAN, PERU

4.1 INTRODUCTION

Maternal aggression, or aggressive behaviour exhibited by females during pregnancy and lactation, is relatively common among mammals (for reviews see Svare 1981, 1990; Maestripieri 1992). The proximate function of this behaviour is thought to be the protection of young (especially neonates) from physical interactions with conspecifics; thus, maternal aggression may ultimately be considered a form of parental investment. Some studies have suggested alternative functions to offspring defence, including defence of nesting areas and materials, maintaining spacing among individuals, establishing dominance hierarchies among females, and avoidance of post-partum fertilization (reviewed in Maestripieri 1992).

In species in which offspring are vulnerable to deliberate or incidental harrassment from conspecifics, maternal aggression is predicted to increase substantially during lactation. In colonially breeding pinnipeds, maternal aggression is prevalent and is most often associated with defence of pups from other adult females, which often threaten or attack non-filial pups (Le Boeuf and Briggs 1977; Christenson and Le Boeuf 1978; Boness *et al.* 1982; McCann 1982; Francis 1987; Ribic 1988; Harcourt 1992; Le Boeuf and Campagna 1994). Female aggression is also associated with competition for space during the breeding season, particularly in species that breed in high densities or in which preferred substrates for nursing are a limited resource (Doidge *et al.* 1984; Carey 1992; Harcourt 1992; Majluf 1992). In addition, female aggression is thought to function in mate choice in northern elephant seals (*Mirounga angustirostris*) and grey seals (*Halichoerus grypus*), by inciting competition among males and thereby increasing the likelihood of mating with a dominant male (Cox and Le Boeuf 1977; Boness *et al.* 1982).

In his study of South American fur seals (*Arctocephalus australis*) breeding at Punta San Juan, Peru, Harcourt (1990, 1991, 1992) found levels of female aggression "several orders of magnitude higher than at any phocid colony, and significantly greater than in other otariid colonies" (Harcourt 1991: 325). Aggression among females at Punta

San Juan appears to be driven to these levels by a combination of high densities within the breeding colonies and the need by females to make daily thermoregulatory movements in response to thermal stress (Trillmich and Majluf 1981; Harcourt 1992; Majluf 1992). This has resulted in the highest average pup mortality recorded in any fur seal population to date, both directly by injury from non-related females, and indirectly due to the "Trauma-Starvation Syndrome" (Le Boeuf and Briggs 1977), in which disturbances within the colony cause separation of mothers from pups, resulting in failure of the mother-pup bond to form (Harcourt 1992; Majluf 1992). Female aggression was lower on less crowded breeding beaches, although these colonies were subjected to predation on pups by South American sea lions (*Otaria byronia*) (Harcourt 1992).

The function and consequences of maternal aggression in South American fur seals at Punta San Juan are clear. However, while observing vocal behaviour in the species during this study, I had the opportunity to explore some social, environmental and ecological factors which might influence the level of aggressive behaviour among females. Specifically, in this chapter I present a preliminary investigation of the potential influence of female interactions with adult males, adult females and pups, as well as the effect of climatic conditions and disturbances caused by sea lions entering the colony for hunting or hauling out. I then compare these influences to factors which might affect female aggression in other species of colonially breeding pinnipeds.

4.2 MATERIALS AND METHODS

4.2.1 Social factors

I used the data on call usage (described in Chapter 3) to calculate call rates (number of calls / individual / hour) for five calling situations involving adult fur seals:

1. agonistic calling among females
2. agonistic calling among males
3. agonistic calling by females to males
4. barking by males to females
5. affiliative calling by mothers to pups

Agonistic calling included all threat and submissive vocalizations (Chapter 3). For the 1995 season, I examined differences between each period within the pupping season for each calling situation. I then used principle components analysis (PCA) to explore relationships among the five calling situations, using the data from the peak periods of 1994 and 1995 only, with a minimum eigenvalue criterion of 1.0. No rotation was required to differentiate among the resulting factors.

4.2.2 Environmental factors

Environmental conditions such as air, sea and black-body temperatures (°C) were recorded daily at 0600, 1200 and 1800 hours, using a hand-held digital thermometer (described in Majluf 1987). Cloud coverage (clear: 0%; haze: 0-33%; cloudy: 33-67%; overcast: >67%) and sea state (calm: no whitecaps; moderate: occasional whitecaps; rough: mostly whitecaps) were estimated by eye at the start of each observation period. Tidal height (m) was estimated by linearly extrapolating from tide tables for the hours of 0730, 1230 and 1700, representing the average midpoint of the observation periods.

Two-way ANOVA (using year as one factor to account for year-to-year differences) were used to confirm the relationship between temperature and time of day (morning, noon or evening). Although mean air and sea temperatures were significantly different between years ($F = 15.21$ (air), 92.90 (sea); $df = 1, 120$; $p<0.001$ for both), all three temperature measurements were significantly higher at midday than in the morning or evening in both years ($F = 166.48$ (air), 72.64 (sea) and 216.38 (black body); $df = 2, 120$; $p<0.001$ for all three). Therefore, the time of day was used categorically to determine the effect of temperature on the rate of calling.

The estimates of tidal heights were not normally distributed, so the values were pooled into four categories describing tidal state (rising, high, falling, low). The distribution of tidal heights was significantly different among categories (Kruskal-Wallis $H = 42.63$, $df = 3$, $p<0.001$). Also, the absolute height of the tide varies both monthly and seasonally and provides no information on the tidal state experienced by the seals; thus, tidal state might be a more important influence on the animals' behaviour.

The effects of time of day, tidal state, sea state and cloud cover on the rate of calling were examined using one-way ANOVA. Because data did not occur in all combinations of the factors, I was unable to consider interaction effects among the environmental variables (for example, using a multifactorial ANOVA or multiple regression design). Instead, I used a PCA (min eigenvalue = 1.0, no rotation) to explore relationships among these four categorical variables.

4.2.3 Sea lion disturbances

Between Oct 05 - Dec 11, 1995, all occurences of sea lions entering the fur seal colony at beach N4 were documented from 0600 to 1800 hours, except for six of these days in which tagging operations precluded observations. Thus, sea lion intrusions were monitored over a total of 60 days (720 observation-hours). For each intrusion, the sex/age class of the sea lion(s) was recorded, and its apparent behaviour discerned from contextual cues. Contexts of sea lion intrusions included *hunting*, in which a sea lion approached the colony in a stealthy manner and moved towards a fur seal pup, as per Harcourt (1993); *hauling out*, in which sea lion(s) hauled out onto the rocks within or adjacent to the colony and laid down; and *sexual behaviour*, in which a pair of adult sea lions hauled out within the colony and attempted to copulate, or in which a male sea lion moved through the colony emitting barks while apparently searching for a female sea lion. I also recorded whether the intruding sea lions attacked fur seal pups, how successful the attacks were and the subsequent behaviour of the sea lion. To assess the effect of the sea lions' presence on the fur seals, I recorded whether the sea lions were challenged by territorial male fur seals, and the reaction of the fur seals in general.

4.3 RESULTS

4.3.1 Social factors

In 1995, the rate of calling generally increased as the season progressed (Figure 4-1), although this increase was only significant for female-male agonistic interactions ($F = 10.33$; df = 2, 144; $p < 0.001$), the rate of barking by males to females ($F = 4.54$; df = 2, 144; $p = 0.01$) and mother-pup calling (t-test on Onset vs Peak periods, $t = 7.21$, $df = 1, 94$; $p < 0.001$).

The results of the PCA suggest that the variables describing social interactions fall into two groups: the four calling situations involving interactions with females loaded together in one factor of the PCA, while the second factor described interactions among males only (male-male agonistic calling) (Table 4-1). Thus, male-male interactions do not appear to be associated with behaviour involving females. Also, male barking to females loaded in the same factor as all female calling, suggesting that the rate of male barking is somehow associated with female behaviour.

4.3.2 Environmental factors

Climatic conditions were relatively constant at Punta San Juan during the peak periods of 1994 and 1995. Air, sea and black body temperatures peaked at midday (Figure 4-2a). The mornings were typically overcast (61%) or clear (27%), but rarely hazy or cloudy, since the cloud cover burned off almost immediately once the sun reached a critical altitude, usually between 0700 - 0800. The sky was usually clear at noon (64%), while the evening was more variable (50% clear, 13% haze, 10% clouds, 27% overcast). Sea state appeared to be independent of all other environmental variables; the sea was classified as calm approximately 60% of the time, moderate 30% and rough 10%, regardless of the time of day or state of the tide. Also, the PCA on the environmental variables resulted in sea state loading on a separate factor from the other variables (Table 4-2).

Both time of day and cloud cover strongly influenced agonistic interactions among females (Table 4-3, Figure 4-2 a,b). In general, females were more agonistic at noon and under clear skies, when insolation (and subsequently thermal stress) was highest. Males also barked significantly more often to females at noon, and the effect of cloud cover on male barking approached significance ($p = 0.06$). The rate of agonistic calling by females to males was also significantly higher under clear skies. In contrast, neither mother-pup calling nor male-male agonistic calling were affected by time of day or cloud cover (Table 4-3, Figure 4-2 a,b).

Sea state had a significant effect on the rate of mothers calling to pups, and on the rate of agonistic calling by females to both females and males (Table 4-3, Figure 4-2c). Females called significantly more when the sea was calm than in any other conditions. Conversely, males appeared to call more during rough seas, although these trends were not significant.

The state of the tide had no effect on any of the calling situations analyzed, although males seemed to bark more often to females at low tide, and mothers appeared to call more often to their pups when the tide was changing (rising or falling) (Table 4-3, Figure 4-2d). However, because tidal state was classified as rising or falling in 102 of 134 searches (76%), the effect of "changing" tide on call rate could not be tested statistically.

4.3.3 Sea lion disturbances

Sea lions entered the colony at beach N4 on at least 85 occasions during the 60 days of observations (range = 0 - 8 intrusions/day; $\bar{x}$ = 1.4 intrusions/day; median = 1 intrusion/day). Of these, over 45% (39 events) involved hunting behaviour, while in 30% (27 events) the sea lions hauled out and rested without overt interactions with the fur seals (Table 4-4). Intrusions involving sea lions engaged in sexual activities accounted for a further 7% of the colony disturbances.

The hunting sea lions were primarily subadult males, and these were almost always challenged by adult male fur seals in nearby territories (Table 4-4, Figure 4-3). Pups were attacked in 12 of 39 (30%) attempts, although pups escaped in half of these. In most hunts, sea lions attacked only one pup and usually retreated to sea with it. However, on one occasion, a subadult male sea lion attacked four pups in sequence, killing and partially eating two of them and mortally injuring (but not eating) the other two before retreating to the sea. The same sea lion, recognizable by a deep cut on its nose, entered the colony almost every day between 12 - 20 Dec (after observations had ended), killing an estimated eight - twelve more pups. Sea lions entering the colony to hunt caused localized disturbances of the colony, ranging from increased alertness to a complete stampede (Table 4-4).

Although not contributing directly to pup mortality, sea lions that hauled out in the fur seal colony, whether for rest or sexual activity, also caused disturbances among the fur seals (Table 4-4). These sea lions were typically adult males with or without a consorting female, and were actively challenged by male fur seals about half the time. On other occasions, territorial male fur seals approached the sea lion(s) and gave full-neck displays (Stirling 1971) but did not threaten them visually or vocally (Figure 4-4). In most cases, the adult sea lions remained within or adjacent to the colony and rested (Table 4-4).

4.4 DISCUSSION

For South American fur seals in Peru, the high levels of female:female aggression recorded by Harcourt (1990, 1991), and subsequently the rate of agonistic calling among females appeared to be influenced by both environmental and social factors. Harcourt (1990, 1992) showed that both increasing ambient temperatures and the level of female activity (measured as # females moving / 15 min and # open-mouth threat displays / female / 15 min) contributed to higher levels of aggression between females in the colony. The results of this study further suggest that a combination of factors such as temperature, level of insolation and choppy seas might increase the level of aggression among females as they attempt to meet their thermoregulatory requirements while protecting their pups from injury. Similarly, Christenson and Le Boeuf (1978) found that aggression among female northern elephant seals was influenced by weather conditions; specifically, the combination of a high tide with winds and high surf caused mothers and pups to become separated, resulting in increased female aggression as mothers attempted to reunite with their pups.

In this study, aggression among females was frequently investigated and even interrupted by adult males, which would approach the females while barking continuously. This behaviour has also been documented for a number of pinniped species (reviewed in Miller (1974)). Harcourt (1990) and Francis (1987) contend that although this behaviour may be obvious to observers, it actually occurs rarely and its significance may therefore be overrated. However, any kind of activity is rare for most territorial male fur seals, since males that conserve energy have the advantage of retaining their tenure longer, thereby increasing their opportunities for mating (Stirling 1971; McCann 1980; Bester and Rossouw 1994). Since barking to females represents more than half the vocalizations produced by males (Chapter 3), I suggest that this behaviour may indeed be significant in terms of the activity budget of territorial males.

Males may also use barking more frequently than threat vocalizations simply because barks are energetically cheap to produce, and approaching females is a low risk behaviour that is potentially advantageous to territorial males. Studies on other pinniped species have suggested that males may use the level of female aggression as a cue to sexual receptivity, since females are thought to be more aggressive at estrus (Cox and Le Boeuf 1977; Gisiner 1977; Boness *et al.* 1982). However, both Majluf (1987) and Harcourt (1990) report no correlation between the timing of estrus and levels of female aggression in South American fur seals at Punta San Juan and, in this study, the rate of agonistic calling among females was not significantly higher during the peak of the pupping season, when most of the females would be near estrus (Figure 4-1). Thus, the apparent association between male barking and female aggression (toward both females and males) observed in this study may be simply a reflection of males' tendency to respond to any disturbance in their territory (Peterson and Bartholomew 1967; Miller 1974; Harcourt 1990). This may also explain why male-male aggression appeared to be independent of calling situations involving females (Table 4-1), since interactions between males typically involve inter-territorial disputes, rather than ongoing behaviour within a male's territory.

High air temperature at midday resulted in higher activity levels in South American fur seals at Punta San Juan (this study; Harcourt 1990, 1991). Other pinnipeds have been found to depress their activity in response to increasing heat (Miller 1974; Christenson and Le Boeuf 1978; Limberger *et al.* 1986; Trites 1990). In many species, once the temperature reaches a critical level of tolerance, males and females alike may abandon the beach for the water (Gentry 1973; Campagna and Le Boeuf 1988; Francis and Boness 1991; Bester and Rossouw 1994). At Punta San Juan, however, females migrate to the tidal area but typically do not leave the colony, possibly because of the high risk of mortality to unattended pups from unrelated females. As Harcourt (1991) suggests, female fur seals at Punta San Juan may be trapped in an unenviable situation in which thermoregulatory movements exacerbate female aggression and subsequent pup mortality, yet to protect her pup, each mother must maintain a high level of aggression while enduring considerable heat stress.

Although heat, movement and other environmental factors affected the levels of female aggression and male barking, those factors had no significant effect on the rate at which mothers called to their pups during the day, which remained relatively high regardless of the environmental factors (Figure 4-2) except sea state (see below). Thus, it might be more efficient for mothers to maintain regular vocal contact with their pups throughout the day, rather than spending time and effort to find pups if they become separated from their mothers (Renouf 1984; Perry and Renouf 1988; Trillmich 1990). It would also increase pups' survival by minimizing the risk of harrassment by other females, a significant source of mortality for young fur seals at Punta San Juan (Harcourt 1991, 1992, 1993).

In this study, females called less as the sea state became rougher (Figure 4-2c). Possibly, the noise produced by heavy surf may interfere with the transmission of fur seal vocalizations on the beach, causing me to underestimate the number of calls produced. Alternatively, since vocal communication is less effective under these conditions, females may reduce their calling rate accordingly to conserve energy. The latter scenario does not seem adaptive, however, since pups are more likely to become separated from their mothers during high seas (Christenson and Le Boeuf 1978; Boness *et al.* 1992). Another possibility is that pups might tend to stay closer to their mothers in rough conditions; if mothers call less when pups are nearby (see Figure 3-8), this might also explain the reduction in mother to pup calling when the sea is rough.

Another factor which may contribute to female-female aggression is disturbance of the breeding colony by land-based predators, in particular those that target pups. Although other species of colonially breeding pinnipeds experience disturbance from predation on pups (Table 4-5), none of them are also subjected to the combination of environmental factors experienced by South American fur seals in Peru. Predation on pups and weaned juveniles at sea may also contribute to seal mortality (e.g. Gentry and Johnson 1981;

Ainley *et al.* 1981, 1985; Jefferson *et al.* 1991), but I have not considered it here since it is unlikely to influence the behaviour of females on the breeding colony. At Punta San Juan, sea lion predation on fur seal pups throughout the breeding season is responsible for up to 5% of pup mortality (Harcourt 1992). However, this figure may underestimate the mortality associated with mother-pup separation caused by disturbances within the colony. During this study, intrusions by sea lions were, on average, a daily event at beach N4, and were not always associated with hunting behaviour. On most occasions, the sea lions' presence caused localized or massive disturbances of the fur seals. For mother fur seals, disturbances such as these would result in a higher incidence of agonistic interactions and an increased risk of becoming separated from their pups. The frequent intrusion of sea lions onto beach N4, whether for hunting or for hauling out to rest, is characteristic of breeding beaches containing few individuals at Punta San Juan; at more populated beaches such as S3, sea lions are prevented from entering the fur seal colony by males defending aquatic territories (Harcourt 1992, 1993). Therefore, female fur seals that breed on beaches that are susceptible to disturbance by sea lions might be expected to exhibit a higher level of aggression than those for which sea lion intrusions are a rare event.

Because of long-term and continuous human disturbance in most coastal areas of Peru, there is little safe habitat available to fur seals, resulting in high breeding densities in the few protected colonies that remain (Majluf 1992). Other pinniped species, including some fur seals, also breed in high densities, but these inhabit relatively cool climates in which females need make few movements during the day in response to heat (Table 4-5). The Galapagos fur seal is another tropical species that needs to make thermoregulatory adjustments, but relatively low breeding densities tend to minimize aggressive encounters among females (Trillmich 1984; Limberger *et al.* 1986; Trites 1990). Other species of fur seal are able to take advantage of terrain bordering the breeding beaches for nursing pups and maintaining greater spacing between individuals (Table 4-5).

Finally, female fur seals at Punta San Juan appeared to use threat calls more frequently and produce a wider range of threat vocalizations than has been recorded for other species of *Arctocephalus* (Chapter 3). In particular, adult females were observed to produce FTCs in response to an intensely threatening stimulus such as an approaching sea lion or human, and other high intensity threats were heard in agonistic encounters among females. In contrast, studies of other species have reported that females only seem to produce a low intensity "threat call" (Table 3-7). I suggest that a combination of ecological, social and environmental factors such as those described in this chapter has probably influenced the disproportionately high level of female aggression experienced by female South American fur seals in Peru.

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Table 4-1. Summary of PCA on variables describing social interactions, showing factor loadings of each variable on the first two factors extracted in each analysis. Variables that loaded highest on each factor are indicated with bold type.

Variable	Factor 1	Factor 2
Female-female agonistic	**0.746**	-0.276
Female-male agonistic	**0.718**	0.046
Male-female barking	**0.700**	0.364
Mother-pup	**0.622**	-0.298
Male-male agonistic	0.114	**0.911**
Eigenvalue	1.96	1.13
Variance explained	39.3%	22.6%
Cumulative variance	39.3%	61.9%

Table 4-2. Summary of PCA on environmental variables, showing factor loadings of each variable on the first two factors extracted in each analysis. Variables that loaded highest on each factor are indicated with bold type.

Variable	Factor 1	Factor 2
Time of day	**-0.680**	0.568
Cloud cover	**0.678**	0.144
Tidal state	**0.646**	-0.019
Sea state	0.347	**0.866**
Eigenvalue	1.43	1.09
Variance explained	36.5%	27.3%
Cumulative variance	36.5%	63.8%

Table 4-3. Results of 1-way ANOVA (F-values) showing effects of environmental factors on each calling situation involving adult South American fur seals. Significant effects are indicated with bold type. *: p<0.01; **: p<0.001

	Time of day	Cloud cover	Tidal state	Sea state
Female-female agonistic	**15.68** **	**7.69** **	1.57	**7.10** **
Female-male agonistic	1.82	**3.82** *	1.65	**8.30** **
Male-female barking	**7.00** **	2.51 [a]	1.02	0.50
Mother-pup	0.05	2.12	1.95	**7.16** **
Male-male agonistic	0.15	0.50	0.32	0.52
df	2, 132	3, 130	3, 131	2, 129

[a] p = 0.06

Table 4-4. Summary of sea lion intrusions into the fur seal breeding colony at beach N4 between Oct 05 - Dec 11 1995 (60 days).

	Context of sea lion intrusion				
	Hunting	Haul-out	Sexual	Unknown	Total
# intrusions	39	27	6	13	85
Sex / age class of sea lion:					
Subadult male	35	3	1	9	48
Adult male	4	6	3	4	17
Adult female	-	3	-	-	3
Adult pair	-	15	2	-	17
# attacks on pups	12	-	-	-	12
# successes (pups taken)	6 [a]	-	-	-	6
# challenged by male fur seals	33	12	4	8	57
Reaction of fur seals:					
No reaction	3	5	-	-	8
Nearest fur seals alert	9	4	2	1	16
All fur seals alert	4	3	3	1	11
Nearest moved, all others alert	16	8	1	7	32
Pups moved, adults alert	2	-	-	-	2
Stampede; beach cleared	4	2	-	4	10
Outcome of sea lion:					
Took pup to sea	6	-	-	-	6
Departed from colony	28	8	6	13	55
Remained at edge of colony	2	10	-	-	12
Moved around within colony	-	4	-	-	4
Went to sleep within colony	-	5	-	-	5

[a] In one of these attacks, four pups were killed (see text).

Table 4-5. Summary of factors that may contribute to female aggression in some colonially breeding pinnipeds.

Species[a]	Climate	Available habitat for nursing	Relative density of females	Females make thermoregulatory movements?	Colony disturbance by predators?[a]	Source[b]
Otariidae						
S. American fur seal (Peru)	tropical	rocks	high	yes	S. Am. sea lions	17, 22, 23, 30
S. American fur seal (Uruguay)	tropical	rocks	variable	yes	---	31, 32
New Zealand fur seal	temperate	rocks	intermediate	no	---	11, 27
Galapagos fur seal	tropical	rocks	very low	yes	---	28, 29
Antarctic fur seal (S. Georgia)	subpolar	tussock grass	variable	no	---	6, 8, 13
Juan Fernández fur seal	temperate	rocks	variable	yes	---	15
S. African fur seal	temperate	sandy beaches	low	yes	jackals, hyaenas	6, 12
Guadalupe fur seal	temperate	caves, rocks	low	no	---	24, 25
Subantarctic fur seal	subpolar	rocks	medium-high	yes	---	3, 4, 26
Northern fur seal	subpolar	flat, rocky shelves	very high	no	Steller's sea lions	16, 34
S. American sea lion	variable	flat, rocky shelves	variable	yes	killer whales	9, 18, 21
Phocidae						
S. elephant seal	variable	sandy beaches	very high	no	killer whales	10, 18, 20, 21
N. elephant seal	variable	sandy beaches	very high	no	---	19, 33
Grey seal	temperate	sandy beaches	low	no	---	1, 2, 5, 14

[a] Latin names for colonially breeding pinnipeds are provided in Chapter 1. Latin names of predators: South American sea lion (*Otaria byronia*); black-backed jackal (*Canis mesmelas*); brown hyaena (*Hyaena brunnea*); Steller's sea lion (*Eumetopias jubatus*); killer whale (*Orcinus orca*).

[b] Sources: (1) Anderson and Harwood 1985; (2) Anderson *et al.* 1979; (3) Bester 1982; (4) Bester and Rossouw 1994; (5) Boness and James 1979; (6) Bonner 1981; (7) Bonner 1985; (8) Boyd 1989; (9) Campagna and Le Boeuf 1988; (10) Condy *et al.* 1978; (11) Crawley and Wison 1976; (12) David 1987; (13) Doidge and Croxall 1984; (14) Fogden 1971; (15) Francis and Boness 1991; (16) Gentry and Johnson 1981; (17) Harcourt 1992; (18) Jefferson *et al.* 1991; (19) Le Boeuf and Briggs 1977; (20) Le Boeuf and Petrinovitch 1974; (21) Lopez and Lopez 1985; (22) Majluf 1987; (23) Majluf 1992; (24) Peterson *et al.* 1968; (25) Pierson 1987; (26) Roux and Jouventin 1987; (27) Stirling 1971; (28) Trillmich 1984; (29) Trillmich 1987; (30) Trillmich and Majluf 1981; (31) Vaz-Ferreira and Palerm 1961; (32) Vaz-Ferreira and Ponce de Leon 1987; (33) White and Odell 1971; (34) York 1987.

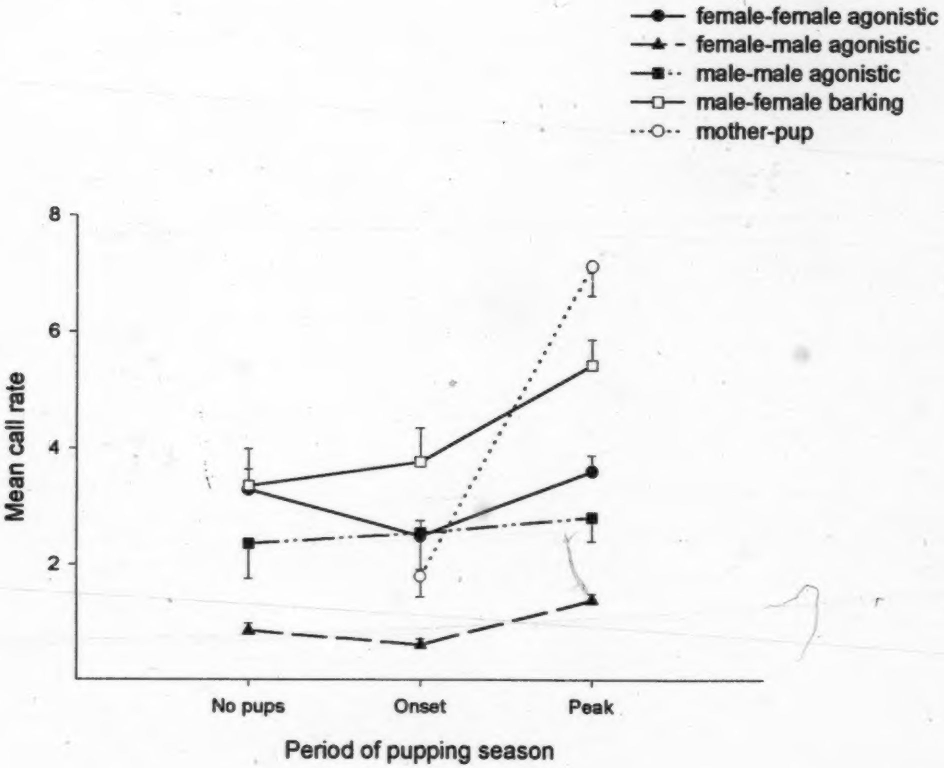

Figure 4-1. Change in calling rate (# calls / individual / hr) during the 1995 breeding season. Error bars represent S.E. of mean; for clarity, only one side of each bar is shown.

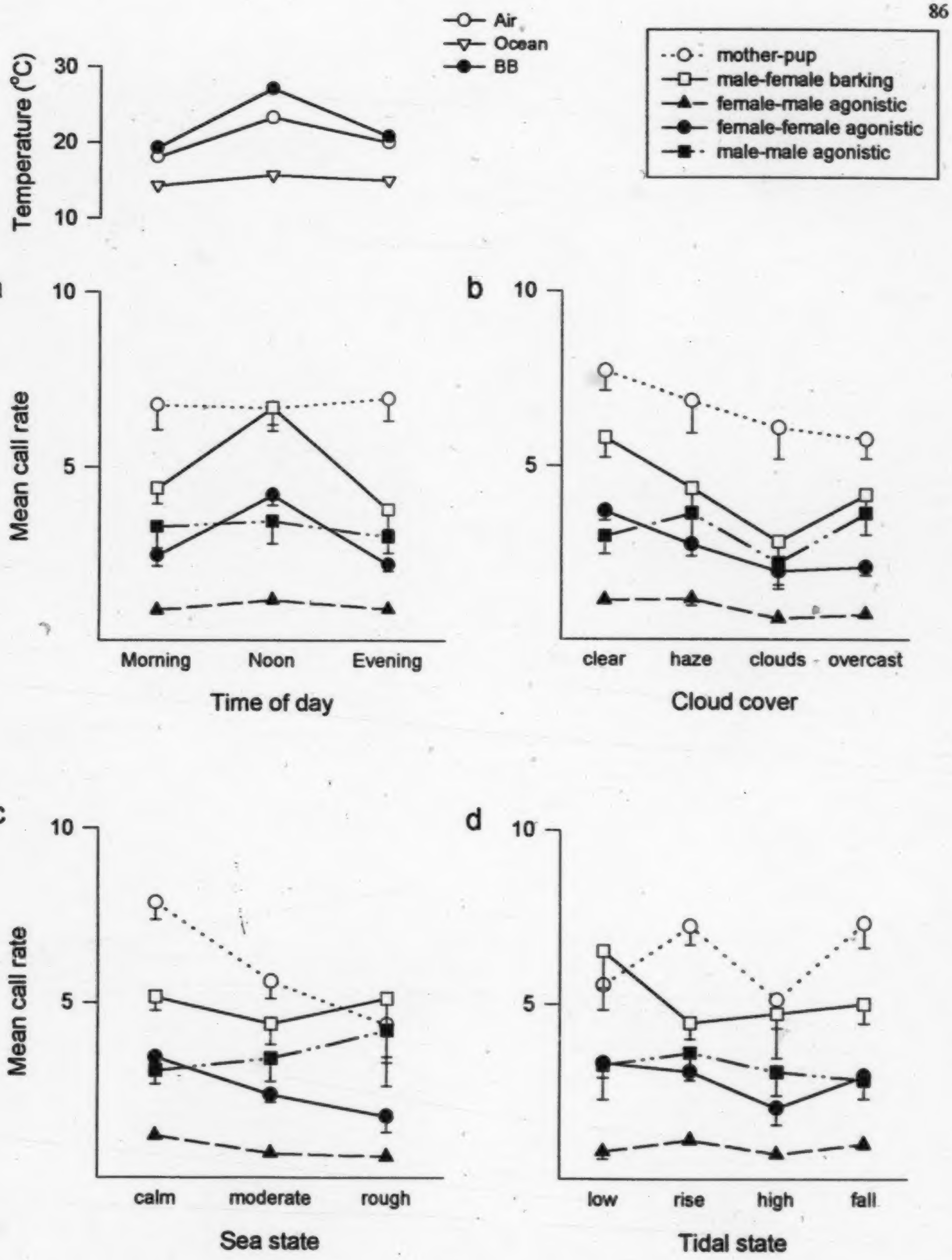

Figure 4-2. Relationships of environmental conditions and calling rate of adult fur seals. The effect of time of day on temperature is shown above a). Error bars represent S.E. of mean; for clarity, only one side of each bar is shown.

Figure 4-3. Subadult male South American sea lion being threatened by two territorial male South American fur seals, after it attempted to steal a fur seal pup. Note that all other fur seals have retreated towards the tide line.

Figure 4-4. Adult male (upper left) and adult female (upper right) South American sea lions hauled out within the fur seal colony at beach N4. Note full neck displays by male sea lion and territorial male fur seal (lower).

5. BEHAVIOURAL CUES USED IN REUNION BETWEEN MOTHER AND PUP SOUTH AMERICAN FUR SEALS

5.1 INTRODUCTION

Parental care has evolved as a means by which animals can attempt to increase the survival of their offspring; however, such an adaptation can be costly in terms of parents' future reproductive success (Trivers 1972; see also reviews in Daly 1990; Clutton-Brock 1991). Parental investment may be particularly high in mammal mothers, because the metabolism of milk for provisioning of young is energetically expensive (Oftedal *et al.* 1987, Clutton-Brock 1991). Some mammalian species raise their offspring communally, and maternal effort is supplemented with input from other (usually related) group members (e.g. lions, *Panthero leo* (Bertram 1976); tamarins, *Saguinus fuscicollis* (Terborgh and Goldizen 1985); coyotes, *Canis latrans* (Bekoff and Wells 1986); see also reviews in Nicolson 1987; Smuts *et al.* 1987; Bertram 1983; Michener 1983). Because in the majority of mammals, mothers provide exclusive care to their offspring, selection for adaptations that would facilitate nursing and minimize misdirection of maternal effort should be expected.

Separation of mothers from offspring increases the cost of rearing young, since mothers must expend energy relocating and reuniting with their offspring. Also, young may experience increased risk of injury or predation while unprotected by their mother, as well as an increasing risk of starvation depending on the duration of the separation event. Le Boeuf and Briggs (1977) refer to this problem as the "Trauma-Starvation Syndrome" (see also review in Gubernick 1981). In species in which mothers leave their young while foraging, numerous adaptations have evolved to facilitate reunion. Infants may be left in a safe location such as a den, burrow, or tree, to which the mother returns to nurse or provision her young (e.g spotted hyaena, *Crocuta crocuta* (Mills 1985, 1989); lesser bushbaby, *Galago senegalensis* (Bearder 1987)). Separation of mothers and young is also common in species that live in large groups (e.g. reindeer, *Rangifer tarandus* (Espmark 1971); bottlenose dolphins, *Tursiops truncatus* (Smolker *et al.* 1993)). For animals that breed in colonies, and in which the young may intermingle while the mother is away, mothers and young must be able to reunite quickly and efficiently, to avoid misdirection of maternal effort and to reduce the amount of time that the infants are alone (e.g. bats: Balcombe 1990; Thomson *et al.* 1985; McCracken and Gustin 1987; pinnipeds: Renouf 1984; Perry and Renouf 1988; Kovacs 1995).

Fur seals and sea lions (Pinnipedia: Otariidae) are an appropriate group for examining the process of recognition and reunion between parents and offspring. Lactation in otariid seals varies from 4 to 12 months but up to 36 months in some circumstances, and therefore represents a major energetic component of maternal effort (Bonner 1984; Oftedal *et al.* 1987; Trillmich 1990; Lee *et al.* 1991; see also reviews in Gentry and Kooyman 1986; Bowen 1991; Boness and Bowen 1996). Pups are born in dense breeding colonies, and after a brief perinatal attendance period, mothers leave their pups in order to forage offshore for several days at a time, returning to nurse for brief periods. Previous studies of otariid behaviour have established that mothers and pups recognize one another by their individualistic vocalizations, and that reunion appears to be mediated by a combination of visual and olfactory cues (Bartholomew 1959; Peterson and Bartholomew 1967; Marlow 1975; McNab and Crawley 1975; Trillmich 1981; Roux and Jouventin 1987; Hanggi 1992; Insley 1992; Schusterman *et al.* 1992). While studies of recognition are numerous, few have attempted to quantify the process of reunion in otariids, such as the use of non-vocal behaviour and the role of the pup in the process (Ono 1972; Gisiner and Schusterman 1991).

For South American fur seals breeding at Punta San Juan, Peru, several factors make it more difficult for mothers to reunite and remain in contact with their pups than is the case for other otariids. The tropical heat causes mothers and pups to make daily thermoregulatory movements to the water's edge in the heat of the day. These movements, combined with the high densities of seals in the breeding colonies result in higher levels of aggression among females than have been recorded for any other species of fur seal (Harcourt 1991a, 1992; Majluf 1992). Mothers and pups are frequently separated by disruptions. While separated from their mothers, pups risk injury from unrelated females, which typically aggressively bite or toss pups they do not recognize as their own. Thus, there are energetic and offspring survival benefits to mothers that are able to quickly locate, reunite with and remain in contact with their pups during onshore attendance periods (Trillmich 1990)

In this chapter, I explore reunion behaviour in South American fur seal mothers and pups, by addressing the following questions: In addition to using vocal cues (discussed in more detail in Chapter 6), do mothers and pups employ other behavioural adaptations to facilitate reunion, and are some of these more successful than others? What are the respective roles of the mother and the pup in the reunion process, and does this change as the pup matures? I begin by describing the reunion process, then examine the various behaviours exhibited by mothers and pups in various contexts.

5.2 MATERIALS AND METHODS

5.2.1 Behavioural observations

During the 1994 breeding season, observations of mother-pup behaviour were recorded *ad libitum*, to qualitatively describe the reunion process and on-beach interactions. In 1995, searching behaviour between mothers and young was documented quantitatively using focal animal sampling over 404 observation-hours, adapted[1] from the methodology of Gisiner and Schusterman (1991). Search and reunion behaviour between mothers and yearlings was recorded between Oct 04 and Nov 25 (265 hrs); these data will be presented elsewhere.

Between Nov 26 and Dec 11 (139 observation-hours), all occurrences of searching behaviour were recorded for mothers that had been tagged in the 1995 season, since bleach marking made their pups more visible (pups bleach-marked in the 1994 season had since moulted and thus I could only detect and recognize them by their numbered flipper tags). Searches of mothers returning from sea were assigned the highest priority for data collection, since the mother's drive to reunite with her pup would likely be highest in that situation. I also documented the behaviour of mothers searching for pups after on-beach separation events of at least 3 female body-lengths, or about 6 m. Previous observations

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[1] Gabriella Battistini and Tanya Luszcz made important contributions to the design of this study.

(Phillips and Stirling, unpubl. data) indicated that mothers appear to lose track of their pups once they are separated by more than this distance, so a search would need to be initiated to reunite the pair.

I defined the beginning of a search as when a female called several times in succession while visually scanning the colony with the neck outstretched (Figure 5-1). Calling was defined as the beginning of a search because behaviour A search was considered to be successful (reunion achieved) when the mother and pup remained together (within ½ female body-length) after making naso-nasal contact. If reunion was not achieved and the female made no further calls for a period of ten minutes, the search was considered to have failed and I used the time of the last call emitted as the end time of the search. For each search, I recorded the following characteristics:

NO_CALLS: number of calls made by the mother
DURATION (min): time of the first call to the time that reunion was achieved or to the time of the last call before the mother stopped calling
CONTEXT: categorized by the mother's behaviour prior to calling:
    sea - mother arrived from offshore foraging
    woke - mother awoke from sleeping on beach
    pool in - mother moved into tidepool
    pool out - mother moved out of tidepool
    other - mother moving around or sitting on beach, awake
HOME: whether the mother visited her "home spot" (see below) while searching
MOVE: whether the mother moved about the colony or remained stationary
SNIFF: whether the mother sniffed at non-filial pups that approached
PUP_CALL: whether the pup responded to its mother by calling
PUP_MOVE: whether the pup responded to its mother by moving toward her
SUCCESS: whether reunion was achieved
OUTCOME: behaviour of pair (or of mother if no reunion) after search:
    suckle - nursing behaviour apparent
    together - pair sitting or lying together, not suckling

apart - pair separated by a distance of at least one female body-length
tidepool - pair swimming together in tidepool
sleep - mother sleeping alone
sit - mother sitting alone, inactive
groom - mother grooming alone
swim - mother swimming alone in tidepool

I defined a home spot as the region (having a diameter of one to two female body-lengths) of the beach that a female frequented most often and in which nursing most often occurred, determined by *ad libitum* observations (Figure 5-2; see also Majluf (1987) and Majluf *et al.* (1996) for descriptions of home ranges on Beach S3 at Punta San Juan).

Under ideal circumstances, playback experiments could be used to estimate the proportion of time that a mother correctly identifies her own pup, or vice versa (for review, see McGregor 1992). Preliminary playback experiments were attempted in 1994, but because the animals were so sensitive to human approach, it was impossible to place a speaker close enough to the animals without disturbing the colony. Therefore, I estimated the *in situ* recognition success rate by noting whether non-filial pups responded to a calling female (indicating incorrect recognition by the pup), and whether the searching female investigated the responding non-filial pup (indicating incorrect recognition by the mother). In this context, pup "response" included calling, orienting or moving toward the searching female.

5.2.2 Statistical analyses

In total, 171 searches by 23 mothers were documented between 25 Nov and 19 Dec 1995. Sample sizes were low for some of the females documented (range = 2 - 15 searches / female), so I restricted the statistical analysis to ten females for which at least eight searches had been recorded (effective total number of searches = 118, including 17 from sea).

In addition to exploring mother and pup behaviours independently, I examined the various behaviours in combinations. Female behaviours were grouped into a categorical variable (STRATEGY), which included eight behavioural combinations: HMS (mother visited home spot, moved while calling and sniffed at approaching pups), HM-, H-S, -MS, H--, -M-, --S and NONE, where dashes indicate that the behaviour did not occur during the search. Note that the arrangement of the three variables does not imply temporal sequence of the behaviours. Similarly, the categorical variable PUP_RESPONSE was used to define pup behaviour, as follows: P-C (pup called to mother but remained stationary), PM- (pup moved toward mother without calling), PMC (pup both moved and called to mother), and NONE (pup was unresponsive to mother's calling).

Because the data set consisted of an unequal number of observations from several individuals, I conducted a preliminary analysis to explore the interdependence of the samples. Both STRATEGY and PUP_RESPONSE were subjected to likelihood ratio tests against female identity and were found to be independent of the identity of the female ($G^2 = 70.73$, $df = 63$, $p = 0.53$ and $G^2 = 41.04$, $df = 36$, $p = 0.06$, respectively), although the test of PUP_RESPONSE approached significance. Since individual females and pups did not appear to use particular behaviours, I considered the samples to be independent. Therefore, the 118 searches could be pooled and analyzed together with little risk of commiting the pooling fallacy (Machlis *et al.* 1985).

I used likelihood ratio tests to explore interrelationships between STRATEGY, PUP_RESPONSE and PUP_AGE. The effect of CONTEXT was explored using likelihood ratio tests for the categorical variables and 1-way Kruskal-Wallis tests for the continuous variables (DURATION, NO_CALLS and CALL_RATE).

To characterize the factors that contribute to the success of a search, I used discriminant function analysis (DFA), a method that distinguishes those variables that contribute most to the variation between successful and non-successful searches. Because DFA is limited to dichotomous or continuous variables, a variable "SEA" was entered instead of CONTEXT to distinguish between mothers returning from foraging trips at sea and on-beach separation events. Missing observations in some cases reduced the sample size to 93 searches for this analysis.

5.3 RESULTS

5.3.1 Overview of the reunion process

Mothers returning from sea generally entered the colony from a central tidepool or a rocky shelf (Figure 5-2: grid coordinates 3D and 8D, respectively), apparently due to the morphology of the shoreline. Regardless of the context of the search, mothers began searching by emitting loud pup-attraction calls, using a stereotypical posture with the anterior part of the body raised high on the foreflippers and the neck and head outstretched (Figures 5-1, 5-3a). Typically, one pup responded to a calling female by orienting or moving towards her and emitting female-attraction calls, although non-filial pups also responded to searching females in 17 of the 94 searches (18%) in which this behaviour was recorded.

Mothers appeared to distinguish their pups by olfactory cues, since naso-nasal contact (Figure 5-3b) always occurred. Females approached and sniffed non-filial pups in 49 of 117 searches (42%; Figure 5-4), but all non-filial pups were violently rejected by being bitten or picked up and tossed aside. Pups that appeared to be accepted became increasingly excited, calling louder and more frequently and usually shaking their heads from side to side and pushing their heads into their mother's neck, head or flank. Once together, the pair typically began nursing (57%, but 92% (12 of 13 searches) when mothers had arrived from sea) or sat together without nursing (32%). When reunion did not occur, mothers typically went to sleep (58%), groomed themselves (19%) or entered a tidepool (17%).

5.3.2 Behavioural characteristics of searches

The majority of mothers visited their home spot while searching, while moving around the colony or sniffing other pups occurred in less than half of the searches (Table 5-1). Pups responded in almost 80% of searches, by calling (73%) and moving toward their mother (68%). Overall, there was no correlation between the behaviour of the mother and that of the pup (STRATEGY * PUP_RESPONSE: $G^2 = 22.36$; $df = 21$; $p = 0.52$) since pups typically responded actively to a search with both movement and calling, while female behaviours were variable. A significant correlation was detected between MOTHER_MOVE and PUP_MOVE, however: when mothers were stationary, pups were much more likely to move ($G^2 = 8.07$; df = 1; $p = 0.004$; Figure 5-5).

The majority of searches took less than ten minutes ($\bar{x} = 8.5$; S.E. = 0.77; range = 0.2 - 33.7 min) (Table 5-1). Most females produced between 10 and 30 calls during a search, although this varied considerably (median = 18; $\bar{x} = 25.5$; S.E. = 2.46; range = 3 - 176). Search duration was linearly dependent on the number of calls produced ($y = 2.75 + 0.22x$; $F = 105.37$; $p < 0.001$), although the number of calls only accounted for 50% of the variance in search duration ($R^2 = 0.50$). Two searches comprised 117 and 176 calls, respectively; however removal of these outliers did not affect the results of any of the analyses. Call rate was (by definition) highly correlated with duration ($R^2 = 0.27$; $p < 0.001$) but not with the number of calls produced ($R^2 = 0.01$; $p = 0.15$).

5.3.3 Effect of context on search characteristics

Almost half the documented searches (46%) were initiated by females that emerged from tidepools where they had been cooling off, while 21% of the searches were initiated when females awoke to find their pup missing (Table 5-2). In the majority of searches, mothers visited the home spot regardless of the context. In contrast, moving and sniffing other pups were affected (albeit weakly) by context (Table 5-2); this was reflected in the test of STRATEGY * CONTEXT ($G^2 = 50.69$; df = 35; $p = 0.049$). For example, mothers seemed more likely to move around the colony when they had arrived from sea, and were most likely to sniff at other pups after coming out of a tidepool (Table 5-2).

Pups did not respond differentially according to the context of the search (PUP_RESPONSE * CONTEXT: $G^2 = 13.34$; df = 15; $p = 0.72$), although pups were slightly more likely to respond when the female was returning from sea or emerging from a tidepool (Table 5-2). Also, non-filial pups were never recorded responding to females coming out of a tidepool (Table 5-2).

When mothers arrived from sea, searches appeared to be shorter in duration, although neither this nor the number of calls produced was statistically significant.

However, females returning from sea called at a significantly higher rate than in any other context (Table 5-2).

5.3.4 Effect of pup age on behavioural characteristics

The estimated ages of pups ranged from 5 to 35 days (median = 15 days). The strategy used by searching mothers was independent of their pups' age ($G^2 = 6.21$; $df = 7$; $p = 0.51$). There were significant differences among pup responses according to the mean age of the pup ($G^2 = 8.57$; $df = 3$, $p = 0.04$), but the variation about these means was large. For example, pups that only moved tended to be younger (5 - 15 days) and pups that only called tended to be older (13 - 24 days), but pups of all ages did both responses (Figure 5-6).

5.3.5 What factors contribute to the success of a search?

Overall, searches were successful about 67 % of the time. Mothers returning from sea had a higher success rate but not significantly higher than the other contexts (Table 5-2). The discriminant function correctly classified over 90% of the searches as successful or non-successful and was a good predictor of those variables which contributed most to the outcome of a search, as shown by the high eigenvalue ($SS_{between} / SS_{within}$) and significantly low Wilk's λ (SS_{within} / SS_{total}) (Table 5-3).

The variables PUP_CALL and PUP_MOVE scored highly on the discriminant function, indicating that the outcome of a search was strongly dependent on the pup's response (Table 5-3). In most searches, pups both called and moved towards the female, a response that led to reunion 95% of the time (100% for seven mother-pup pairs; range 50 - 100%) (Figure 5-7a). In contrast, reunion was achieved in only two (9%) of the 23 searches in which the pup made no response at all.

Successful searches were significantly shorter in duration, and had higher call rates than searches in which mother and pup did not reunite, while the number of calls produced did not influence the success of the search (Table 5-3). Although CALL_RATE showed greater differences between successful and non-successful searches, DURATION loaded strongly on the discriminant function, suggesting that DURATION likely contributes more to the variation in the sample (Table 5-3). The high correlation between NO_CALLS and DURATION may explain why NO_CALLS loaded high on the discriminant function, but was not significantly correlated with the function (R = 0.03).

It appears that PUP_AGE has very little role in the success of a search (Table 5-3). Older pups seemed to be associated with successful searches, although this was not statistically significant. PUP_AGE scored low on the discriminant function and was not strongly correlated with the discriminant function (Table 5-3).

Neither SEA nor the behaviour of the female (HOME, MOVE, SNIFF) were found to be important in discriminating between successful and non-successful searches (Table 5-3). Thus, the discriminant function analysis supports that, assuming the mother returns to the natal beach, the combination of behaviours she used while searching had no effect on the outcome of the search, while the response of the pup is critical for reunion to be achieved (Figure 5-7).

5.4 DISCUSSION

The process of reunion between South American fur seal mothers and pups in Peru is similar to descriptions of other otariid species (Peterson and Bartholomew 1967; Sandegren 1970; Marlow 1975; McNab and Crawley 1975; Trillmich 1981; Insley 1989; Gisiner and Schusterman 1991; Schusterman *et al.* 1992; see also review in Bowen 1991). Mothers and pups use a combination of geographic, visual, auditory and olfactory cues to relocate and reunite with each other.

South American fur seals use geographic location as a cue for reunion at two different scales. At the large scale, females consistently return to the same beach or colony at Punta San Juan to find their pups. Many land-breeding pinnipeds have also been noted to display fidelity to pupping sites, returning to the same colony year after year (Bartholomew 1959; Lunn and Boyd 1991; Pomeroy *et al.* 1994). This is likely facilitated by spatial memory and familiarity with local surroundings and topography, especially for the non-migratory South American fur seals breeding along the Peruvian coast. Thus, mothers have the ultimate responsibility for ensuring reunion, by returning to the correct breeding colony (Peterson and Bartholomew 1967).

At a smaller scale, searching mothers frequently oriented to their "home spot" and nursed their pups there. This behaviour appears to be common among pinnipeds in which mother and pup are regularly separated; other studies have also demonstrated that mothers return to the spot where they last suckled, or consistently return to a discrete area of the beach such as a boulder, tidepool or mound of tussock grass to find their pups (e.g. Bartholomew 1959; Fogden 1971; McNab and Crawley 1975; Trillmich 1981; Lunn and Boyd 1991).

Geographic location is considered a primary cue for reunion in ice-breeding phocids, which have been found to orient to a particular location air hole or ice lead to reunite with their pups. This behaviour seems adequate for location of pups because pups generally do not move far from their birth site (harp seals, *Phoca groenlandica* (Terhune *et al.* 1979; Renouf *et al.* 1983; Renouf 1984; Kovacs 1995); Weddell seals, *Leptonychotes weddelli* (Tedman and Bryden 1979)). For colonially breeding pinnipeds, however, geographic and spatial cues might be most useful for generalized orientation of the pup to its mother because of the density of the breeding colonies (Peterson and Bartholomew 1967). In this study, even though mother South American fur seals frequently returned to their customary home spot, females that used that behaviour were no more successful than mothers who did not go near the home spot (Figure 5-7b). This may be due to the relatively small area inhabited by the colony at Beach N4 (approximately 35m x 15m), since otariid pups can likely hear their mothers' high-pitched calls from a distance of at least 100 m (Marlow 1975; Moore and Schusterman 1987; Renouf 1991). On breeding beaches that cover a larger area and have more animals contributing to the background noise, it might be difficult for pups to hear and localize their mothers' pup-attraction calls, so returning to a home spot might play a larger role in a mother's success in finding her pup.

Visual cues appear to play a role in orienting pups to searching females, since most pups oriented to the distinctive posture and facial expression of searching females (Miller 1975). The dark and shiny coat of wet females may provide pups with further cues. After on-beach separation, pups called somewhat more to females that emerged from tidepools compared to females that were dry. Similarly, pups may provide visual cues that would help mothers to locate them simply by moving towards them (Terhune *et al.* 1979; Kovacs 1995). The low visual acuity of seals in air, however, would likely preclude any finer level of discrimination by visual cues (Renouf 1991). Additionally, attendance records of tagged mothers showed that of 66 returns from sea documented between Nov 01 - Dec 10, 1995, 38 of these (58%) occurred during the night. Similar trends were noted by Trillmich *et al.* (1986) and Majluf (1987). This probably explains the low incidence of searches in which mothers returned from sea in my study. More importantly, because visual cues would be less effective at night, the importance of visual cues may be less than I have suggested.

The response of the pup strongly suggests that pups can discriminate between the pup-attraction calls of their mother and those of unrelated females, even at the young ages of pups in this study. Pups appeared to make errors in identification only 15% of the time, while 77% of the time, the correct pup responded to its mother. This is similar to the low incidence (9%) of "false alarms", or wrong pups responding to calling females, recorded by Gisiner and Schusterman (1991) for California sea lions (*Zalophus californianus*). Playback experiments also demonstrated that subantarctic (*A. tropicalis*) and Galapagos (*A. galapagoensis*) fur seal pups recognize and respond to the pup-attraction calls of their mother, and rarely respond to calls of non-related females (Trillmich 1981; Roux and Jouventin 1987). In most species, the risk to pups associated with approaching unrelated females is high compared to the potential benefit of stealing milk (see Roux 1986 and Lunn 1992). Thus, pups that can recognize mothers from a distance via vocal cues are more likely to avoid being injured (Harcourt 1991a, 1992).

In contrast, searching females approached and/or sniffed non-filial pups in 42% of searches (Figure 5-4). Since pups that are alone present no risk to females, inspecting pups that approach would likely supplement the searching behaviour of females. Olfactory cues appear to be the definitive cue to identification of the pup by its mother in all otariid species (for review see Bowen 1991), although there is little experimental evidence to support this. Roux and Jouventin (1987: 97) sprayed eau de cologne on the head and back of fur seal pups and reported that "nuzzling behaviour was inhibited" but pups were still accepted by mothers if they vocalized. In other studies, pups were marked with "a strong-smelling alcoholic solution" (Fogden 1971: 77) or sprayed with a pine-scented deodorizer to the mouth and nasal areas (Terhune *et al.* 1979); mother seals did not seem to behave differently towards marked or unmarked pups.

The mechanism by which mother fur seals use olfactory cues to recognize their pups remains unknown. Studies of other mammal species have suggested that mothers "label" their offspring, either by pre-natal transfer or licking and grooming after birth. The mothers may then use phenotype matching to recognize their offspring's scent based on similarity with their own (goats: Klopfer 1971; Gubernick 1980; Mexican free-tailed bats, *Tadarida brasiliensis mexicana*: Gustin and McCracken 1987). Scent glands are poorly developed in pinnipeds and it is unlikely that specific olfactory compounds are produced. Also, pinniped mothers do not lick or groom their young, so postnatal labelling would be limited to nuzzling. Mothers may associate the scent of the amniotic sac with their pup, or may simply recognize the scent of their pup by a combination of odours produced by urine, feces, saliva or breath, (Müller-Schwarze 1983; Halpin 1986, 1991). Additionally, as Gould (1983: 281) suggested, "hormonal conditions at birth might alter a mother's sensitivity to her infant by affecting peripheral sensitivity", although the role of the endocrine system in behaviour of pinnipeds is relatively unexplored (Wartzok 1991).

Pups clearly play an active and important role in the reunion process, since pups that responded almost always reunited with their mothers, while passive pups were usually not reunited (Figure 5-7a). Similar results have been reported for California sea lions (Gisiner and Schusterman 1991) and northern elephant seals (*Mirounga angustirostris*, Le Boeuf and Briggs 1997; Riedman and Le Boeuf 1982). The role of the pup is likely underestimated in this study, since I did not record searches that were initiated by pups. Gisiner and Schusterman (1991) reported that pups up to two weeks of age initiated searches 4.5 % of the time, and that this increased to over 10% of the time for four- to six-week old pups. Similarly, Harcourt (1990) demonstrated that over the first 25 days, South American fur seal pups became increasingly more responsible for maintaining proximity of the pair. Although my study included pups of approximately the same age range as Harcourt's, I detected only weak effects of pup age on pup behaviour and success rate (for searches initiated by mothers). The most plausible explanation is that even though the ability of pups to recognize and respond to their mothers likely increases with age, pups also become more mobile, spend more time engaged in play behaviour, and are less dependent on their mothers for protection. Thus, older pups may be less motivated to facilitate reunion unless hungry (Farentinos 1971; Arnold and Trillmich 1985; Harcourt 1990, 1991b; Gisiner and Schusterman 1991).

Although not statistically significant, the results of this study suggest that reunions involving mothers returning from foraging trips at sea may differ from on-beach searches. Pups responded more often to mothers arriving from sea, and these mothers were more successful at reuniting than those searching for their pups after on-beach separation events (Table 5-2). Females coming from sea called at a significantly higher rate and reunion tended to be achieved in shorter times than for on-beach searches. Also, 12 of 13 (92%) searches from sea resulted in suckling within the first five minutes after reunion, compared to 31 of 62 (50%) on-beach searches. These findings suggest that hunger may motivate pups to respond strongly to mothers returning from sea, while maintaining proximity once the pup has suckled may be a lesser priority (Trillmich 1990; Arnold and Trillmich 1985).

In summary, both mother and pup South American fur seals use a variety of behavioural cues to increase the chances of finding one another. However, each appears to be acting under different selective pressures. There is strong selection on the pup to be able to recognize its mother's call from a distance to avoid being injured by unrelated females. The pup must also advertise its presence to its mother and incite her to continue calling so that it can find her quickly. For mothers, it may be advantageous to consistently return to a familiar location on the beach while calling, thus providing the pup with additional geographical and spatial memory cues. There also seems to be no disadvantage to females in supplementing the calling with other behaviours such as moving about the colony or sniffing approaching pups.

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Table 5-1. Characteristics of searches of ten South American fur seal mother-pup pairs.

# searches	118
% successful	66.7
% from sea	15.0
$\bar{x}$ number of calls made by female	25.5
$\bar{x}$ duration of search (min)	8.5
$\bar{x}$ call rate of female (calls/min)	4.5
Mother behaviours:	
% visited home	76.3
% moved around colony	48.7
% sniffed other pups	41.9
% performed none of these behaviours	7.7
Pup response:	
% responded to mother (call and/or move)	77.5
% called to mother	72.8
% moved toward mother	67.6
% wrong pup responded to female	14.4

Table 5-2. Effect of searching context on characteristics of searches. With the exception of "% searches by context", all proportion data represent the proportion of searches in which the behaviour occurred; thus neither rows nor columns total to 100%.

	Context						
Search characteristics	Sea	Woke	Out of tidepool	Into tidepool	Other	Test statistic [a]	p
Number of searches by context	17	24	52	11	9		
% searches by context	15.0	21.2	46.0	9.7	8.0		
$\bar{x}$ number of calls by female	24.6	15.4	28.4	15.7	33.0	7.75	0.10
$\bar{x}$ duration of search (min)	5.7	6.7	9.9	7.8	10.7	4.43	0.35
$\bar{x}$ call rate of female (calls/min)	6.3	4.0	4.5	2.7	4.0	10.22	0.04
% successful by context	76.5	58.3	67.3	45.5	75.0	3.74	0.45
Mother behaviour:							
% visited home	70.6	87.5	76.9	54.5	66.7	5.06	0.33
% moved around colony	76.5	37.5	48.1	63.6	25.0	9.53	0.07
% sniffed other pups	35.3	20.8	55.8	36.4	37.5	9.32	0.06
Pup response:							
% called to mother	85.7	60.0	73.9	66.7	66.7	3.14	0.55
% moved to mother	71.4	60.0	66.7	66.7	66.7	0.51	0.99
% wrong pup responded to female	20.0	16.7	0.0	22.2	16.7	3.33	0.50

[a] Proportion data: likelihood ratio tests (G^2); continuous data (number of calls, duration, call rate): Kruskal-Wallis tests (U); all tests with df = 4.

Table 5-3. Summary statistics for the discriminant function for successful versus non-successful searches.

	Function 1		Comparison of successful vs. failed searches [c]			
Variable	Loading [a]	Pearson R [b]	Success ($\bar{x}$) [d]	Fail ($\bar{x}$)	F	p
PUP_CALL	0.797	0.82	.94	.19	126.65	< 0.001
PUP_MOVE	0.353	0.53	.85	.22	52.00	< 0.001
CALL_RATE	0.034	0.27	3.98	2.29	13.19	< 0.001
DURATION	-0.671	-0.22	6.80	11.87	9.20	0.003
PUP_AGE	-0.087	0.15	18.58	15.37	3.95	0.050
SEA	-0.008	0.10	.18	.07	1.73	0.191
MOVE	0.031	-0.06	.45	.56	0.77	0.382
SNIFF	-0.092	-0.06	.39	.48	0.59	0.443
NO_CALLS	0.465	0.03	25.20	23.26	0.16	0.693
HOME	0.063	-0.02	.76	.78	0.04	0.837
% calls correctly classified	90.32					
Eigenvalue	2.06					
Canonical correlation	0.82					
Wilk's λ	0.33					
Chi-square (df = 9)	96.30					
Significance	< 0.001					

[a] Standardized canonical coefficients, describing loading of each variable on Function 1.

[b] Correlation between each predictor variable and the discriminant function.

[c] One-way ANOVA on each predictor variable with SUCCESS as a group variable (df = 1, 91).

[d] Means for proportion data represent the proportion (%) of searches in which the behaviour occurred.

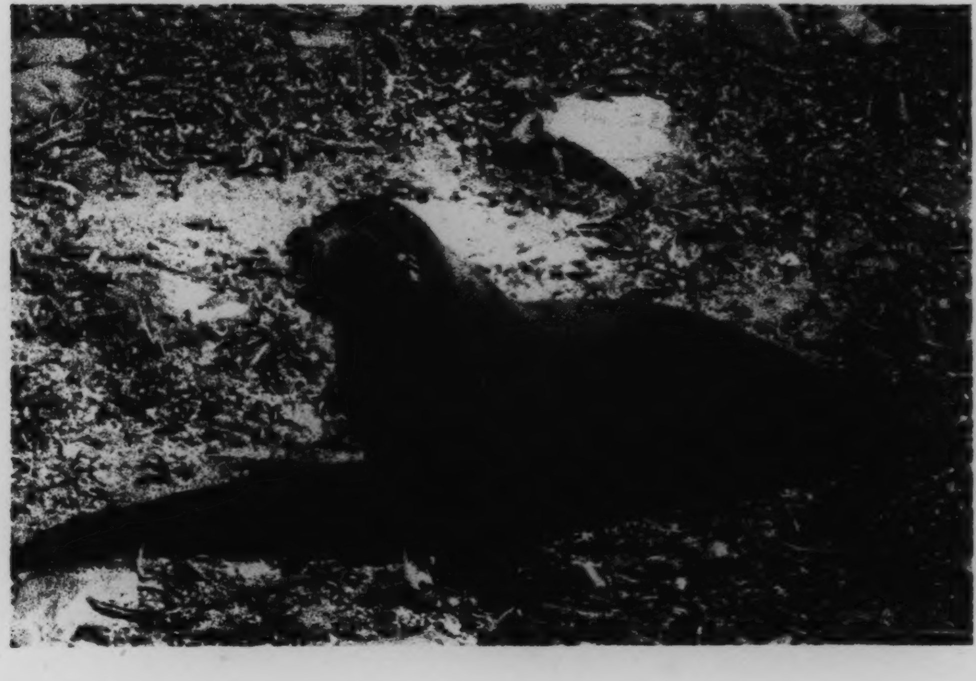

Figure 5-1. Mother South American fur seal emitting pup attraction calls during search for pup after on-beach separation. Note elevation of head, extension of neck and wide open mouth.

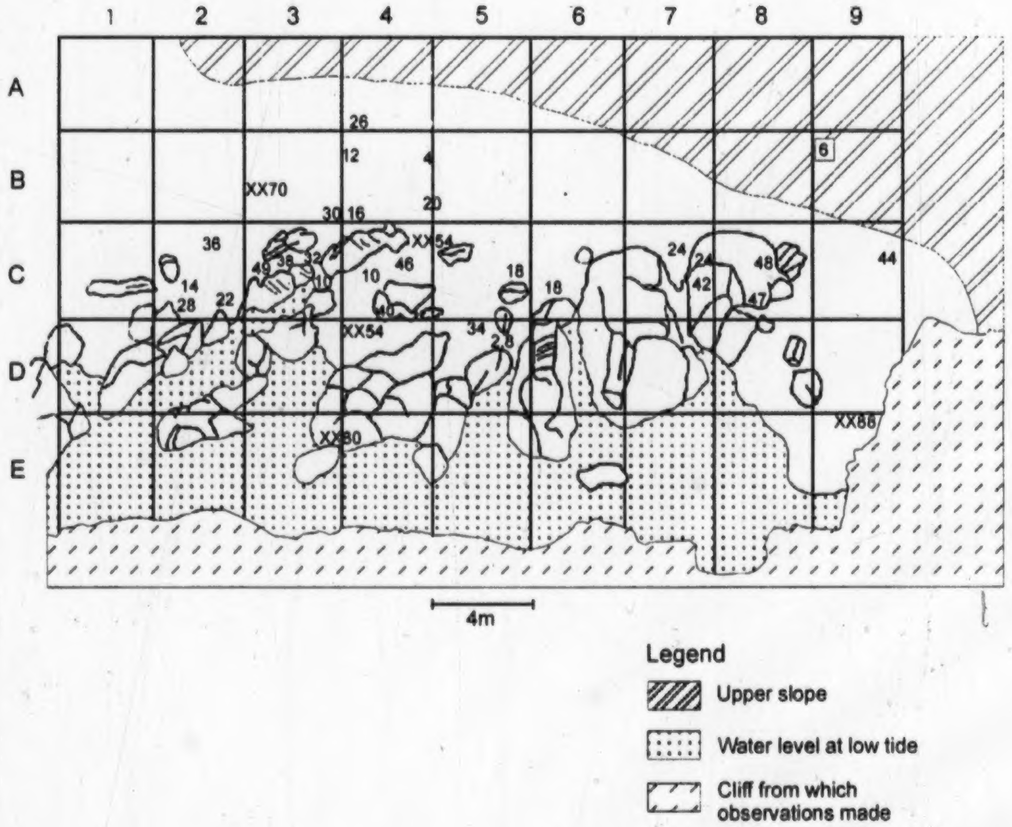
1
2
3
4
5
6
7
8
9
A
B
C
D
E
26
12
4
XX70
20
30
16
XX54
36
49
38
32
10
46
10
14
28
22
40
XX54
18
18
34
2
8
24
24
42
48
47
6
44
XX88
XX80
4m
Legend
Upper slope
Water level at low tide
Cliff from which observations made

Figure 5-2 Location of "home spots" used by tagged mother fur seals at beach N4 in 1995 (same orientation as Figure 2-3). For clarity, the prefix "N4" has been left off the tag numbers that start with this designation. Note that females N410, N418 and N424 appeared to spend equal amounts of time in two adjacent home spots.

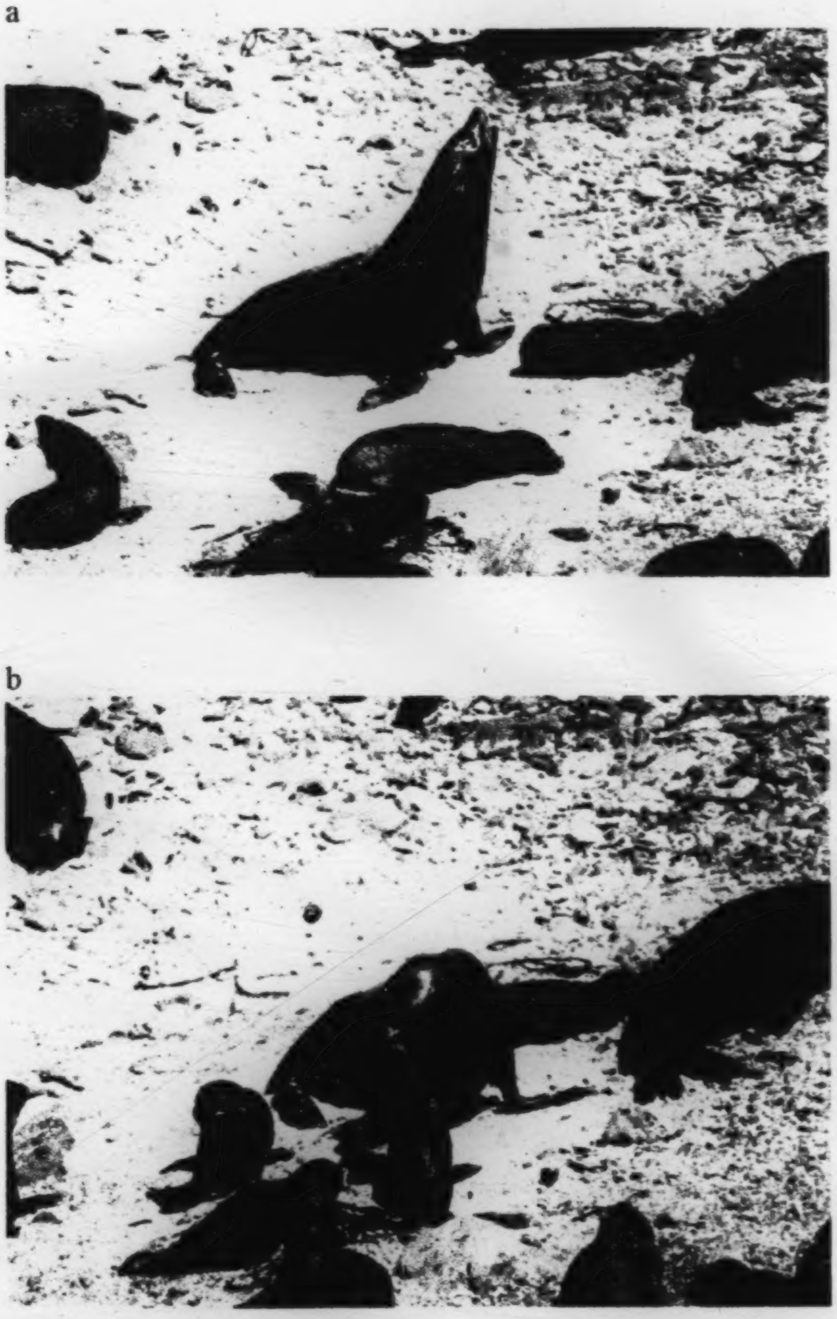

Figure 5-3. a) South American fur seal mother searching for pup after returning from sea. b) Naso-nasal greeting between mother and pup fur seal; note forward extension of vibrissae.

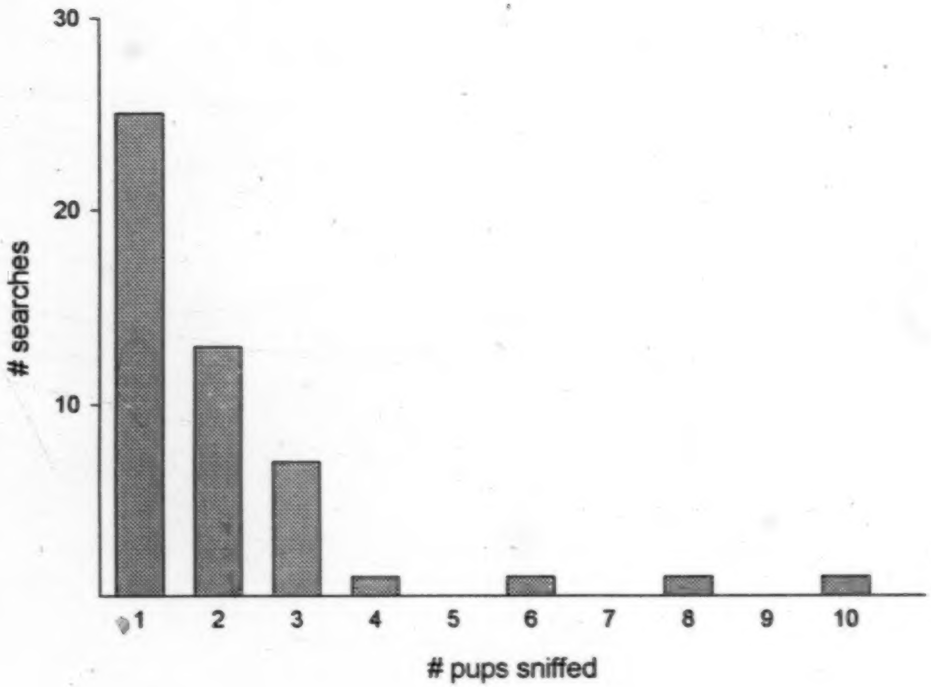

Figure 5-4. Number of non-filial pups sniffed by searching fur seal mothers, of the 49 searches in which this behaviour occurred.

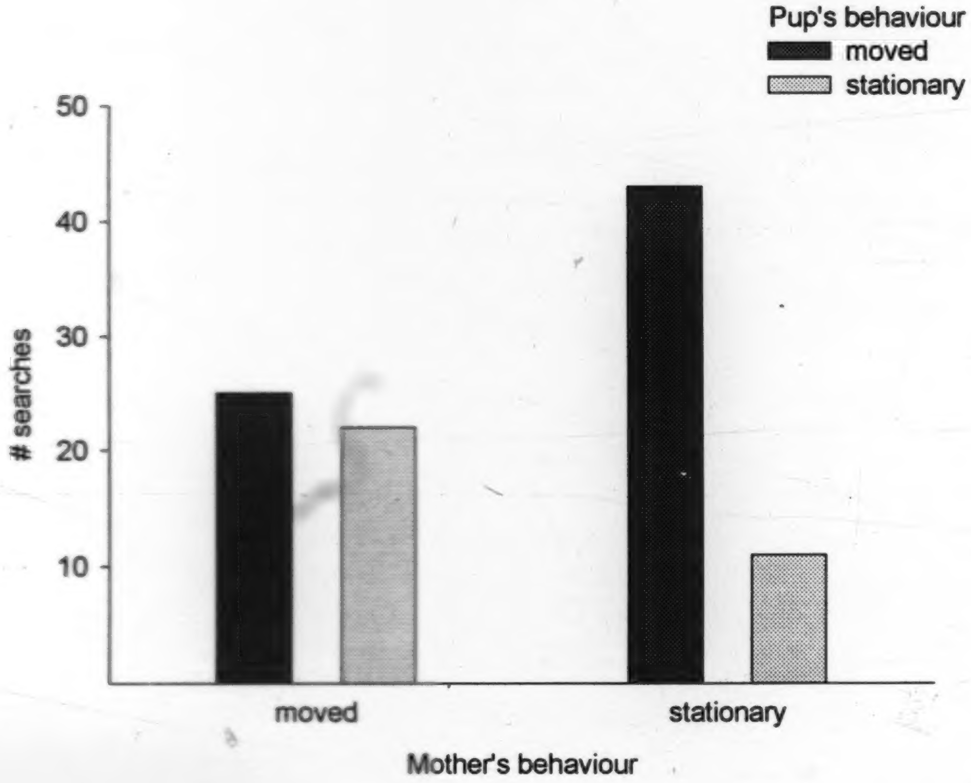

Figure 5-5. Relationship between movement of mother and pup South American fur seals during searches.

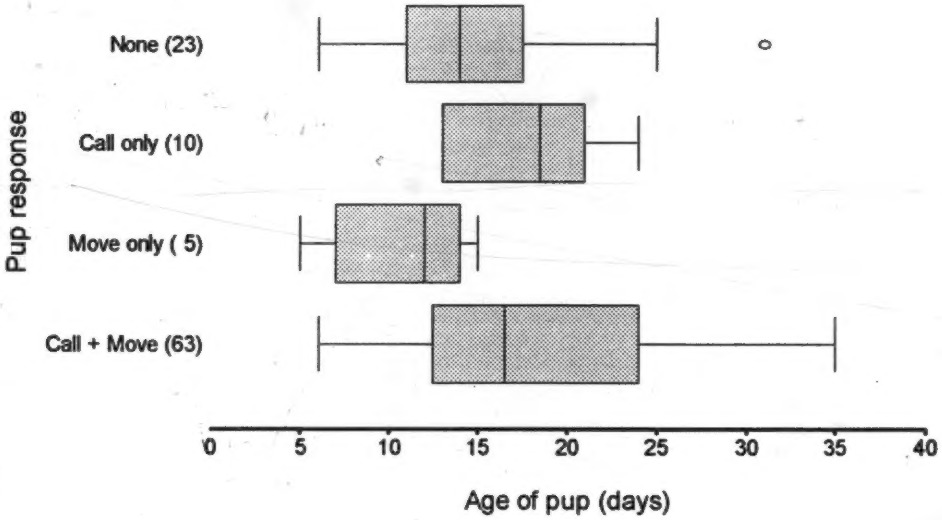

Figure 5-6. Effect of pup age on the distribution of South American fur seal pup responses to searching mothers. Number of searches in which behaviour occurred is shown in brackets. Shaded boxes contain 50% of the values; vertical bar represents median; horizontal bars include all other values that are not outliers; o = outlier.

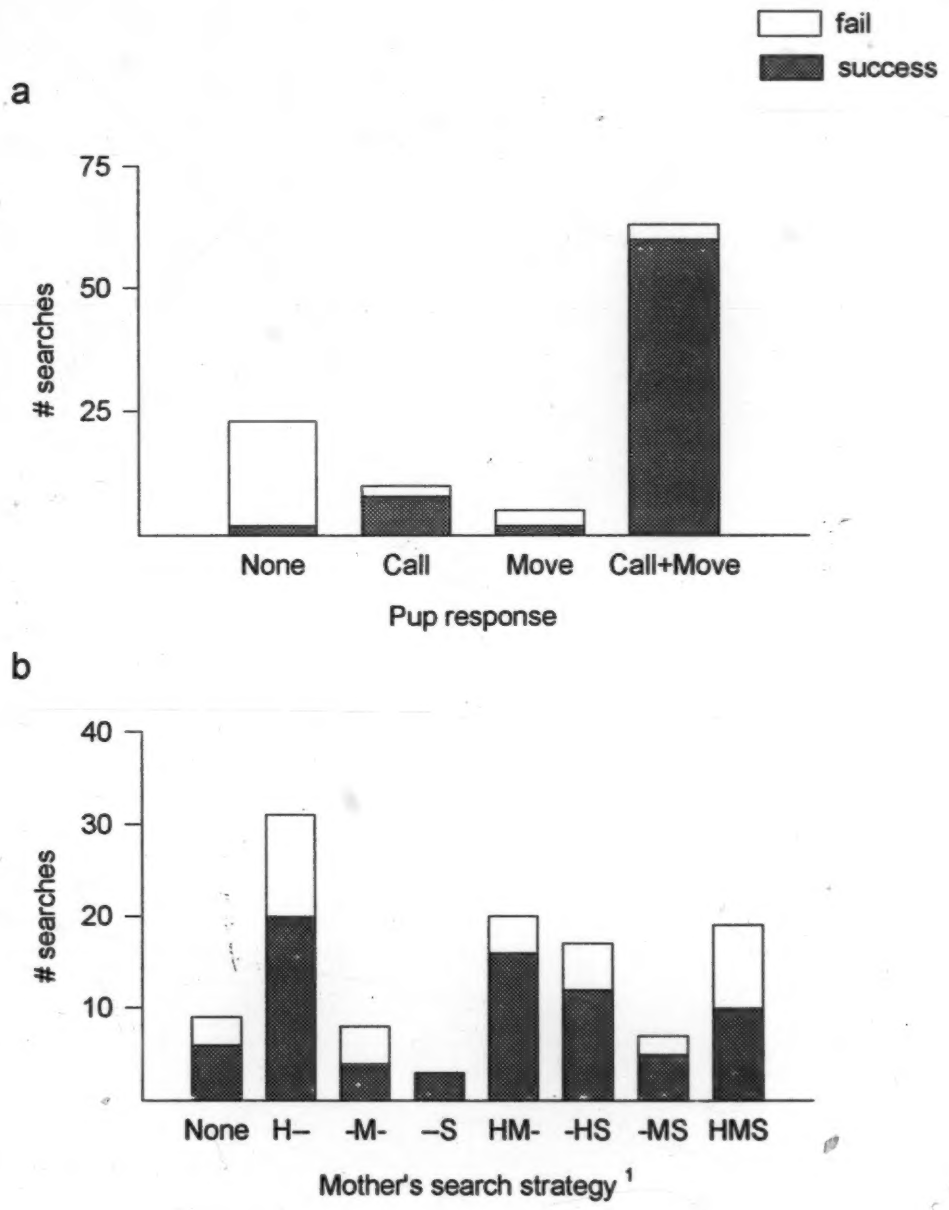

Figure 5-7. Frequency and success rate of behavioural strategies exhibited during searches by a) pup and b) mother South American fur seals. [1]See text for explanation of abbreviations.

6. VOCAL INDIVIDUALITY IN MOTHER AND PUP SOUTH AMERICAN FUR SEALS

6.1 INTRODUCTION

In many species of colonially breeding birds and mammals, parents continue to provision their offspring even after the increasingly mobile young have begun to intermingle with unrelated juveniles. When parental behaviour incurs considerable costs, such as high energy demands or increased risk of predation, misdirecting parental effort lowers the reproductive success of an individual. Thus, selection favours parents that discriminate among offspring and exclusively provision their own (Trivers 1972, see also review in Clutton-Brock 1991).

The ability of parents to recognize their young relies on offspring having distinct vocal signatures, in which the variability between individuals is much greater than within (Beecher 1982). Signature recognition between parents and offspring has been demonstrated in several species of colonially breeding birds and mammals, including Adélie penguins (*Pygoscelis adeliae*, Falls 1982), bank swallows (*Riparia riparia*, Beecher *et al.* 1986), Mexican free-tailed bats (*Tadarida brasiliensis mexicana*, Balcombe and McCracken 1992), evening bats (*Nycticeius humeralis*, Scherrer and Wilkinson 1993) and vervet monkeys (*Cercopithecus aethiops*, Cheney and Seyfarth 1980). Although visual and olfactory cues may enhance individual signatures in these species, vocalizations are typically the primary cue by which parents and offspring recognize one another (Stoddard and Beecher 1983; Gustin and McCracken 1987).

Fur seals and sea lions (Pinnipedia: Otariidae) congregate on crowded breeding beaches, and mothers forage throughout the lactation period, leaving their pup alone for several days at a time. Mothers and pups appear to distinguish each other using vocal cues. Playback experiments have provided evidence in support of mutual vocal recognition; in both the Galapagos fur seal (*Arctocephalus galapagoensis*) and the subantarctic fur seal (*A. tropicalis*), mothers and pups responded positively to recordings of each other's calls but not to those of strangers (Trillmich 1981; Roux and Jouventin 1987). Although these and other studies (Bartholomew 1959; Stirling and Warneke

1971; Trillmich 1981; Trillmich and Majluf 1981; Roux and Jouventin 1987; Schusterman *et al.* 1992) have suggested that there is sufficient call stereotypy to enable individual recognition, the degree of individuality of otariid calls has been quantified only for the northern fur seal (*Callorhinus ursinus*) (Insley 1989, 1992).

In South American fur seals (*A. australis*) breeding at Punta San Juan, Peru, selective pressures for mothers and pups to recognize one another appear to be strong. Colonies are typically dense and intense solar radiation drives animals to make thermoregulatory migrations to the water's edge, causing a high incidence of agonistic interactions as females move through the colony (Trillmich and Majluf 1981). These factors, combined with predation pressure from South American sea lions (*Otaria byronia*), have resulted in levels of female aggression and subsequent pup mortality higher than has been recorded for any other otariid species (Harcourt 1991, 1992; Majluf 1992). Female aggression contributes to pup mortality directly, as females frequently inflict injuries on non-filial pups, and indirectly, through disturbance resulting in separation of mother and pup, leading to failure of the mother-pup bond to form and subsequent starvation of the pup (Harcourt 1991, 1992; Majluf 1992). I hypothesized that these factors would lead to selection for female calls to be highly individualistic, to enable pups to recognize their mothers from a distance, thus reducing the need for pups to expose themselves to danger by approaching females too closely. Similarly, since maternal care might be more costly for South American fur seals compared to other otariid species, pup calls should also be strongly stereotypical, to facilitate rapid reunion between mother and pup and minimize misdirection of maternal effort.

6.2 MATERIALS AND METHODS

6.2.1 Terminology

This chapter refers exclusively to pup-attraction calls (PACs) and female-attraction calls (FACs) made by mother and pup South American fur seals, respectively. For brevity, therefore, my use of the term "call" in this chapter refers only to PACs and FACs. Also, the term "female" refers to adult females; I did not consider sex differences among pups in this study. I use "mother" only when a matrilineal relationship was known. A glossary of acoustic terms is provided in Appendix B.

6.2.2 Recording and acoustic analyses

Recordings were made from the cliff-top observation point at beach N4 during the 1994 and 1995 breeding seasons. After reviewing the tapes, I selected female and pup calling bouts which contained at least 20 calls per individual. I conducted preliminary analyses to examine the effects of two potential biases (pup age and recording context) on the variability of individuals' calls. Based on these, pup calls were taken only from bouts in which the pup was at least 8 days old (Appendix C), whereas it was not necessary to limit the sample of female calls to those from a particular context (Appendix D).

Using the criteria for selection of individuals determined by the preliminary analyses, I chose 15 females and 13 pups for the analysis of individuality. Of these, 10 females and pups were mother-pup pairs. To control for the possible interdependence of calls within a bout, I randomly selected 20 calls from all of the bouts recorded for a particular individual, except where an individual was only recorded on one occasion. Thus, the sample size for each individual was 20 calls, although occasional missing values reduced this value for some variables. I rejected calls that were lost in background noise or saturated due to high recording levels.

Spectrographic analyses were conducted using the SIGNAL/RTS sound analysis package (Engineering Design, Belmont, Mass.). Each call was sampled at a rate of 20 kHz over the frequency range 0 - 8 kHz. Sound spectrograms were calculated in both RTS and SIGNAL from 512-point Fast Fourier Transforms (FFTs), with a corresponding frequency bandwidth of 39 Hz.

The criteria used in measuring each variable are described in detail in Appendix E. Briefly, for each spectrogram I recorded the presence or absence of harmonic structure (TONAL), pulsing (PULSE) and rhythmic frequency modulation (FM) in the call. Eight acoustic features (Figure 6-1a) were then measured in RTS, using on-screen cursor measurements over a frequency scale of 0 - 4000 Hz. These included call duration (DUR), number of parts (structurally distinct regions of a call) (NPARTS), harmonic interval (HI), and the frequency of the lowest visible harmonic at the onset (INF), highest point (MAXF) and end (ENDF) of a call. When FM was present, the period (FMP) and range (FMR) of the modulation was also measured (Figure 6-1a).

An additional five acoustic variables (Figure 6-1b) were measured from power spectra in SIGNAL. These were the frequencies of the first three energy peaks (or amplitude-emphasized frequencies) of a call (PEAK1 - PEAK3), and the relative amplitude of the second and third peaks to the first (AMP2 and AMP3). Power spectra were calculated using 32 K point FFTs averaged over at least 95% of the call duration, smoothed with a 100 Hz window, and displayed with a frequency bandwidth of 0.6 Hz.

6.2.3 Statistical analyses

To improve normality, the square root of NPARTS was used in the analyses instead of raw counts, although results are reported in the original form (Sokal and Rohlf 1981). The categorical variables TONAL, PULSE and FM were combined into a new variable describing call "SHAPE", consisting of five possible states: Tonal, Pulsed, Tonal+FM, Tonal+Pulsed, Tonal+Pulsed+FM. No order of complexity was attributed to these categories. The variable SHAPE was analysed separately from the continuous variables. Missing values were an unavoidable problem when acoustic features were absent or obscured in a call, especially with HI, FMP and FMR, which (by definition) were not present if a call had no tonal components. Missing values were not treated as zeroes, however, as this would have severely skewed the data.

Relationships among acoustic variables were explored using principal components analysis (PCA), which groups correlated variables into factors thereby identifying the acoustic variables which contribute most to the variation of calls in the sample. I used a minimum eigenvalue criterion of 1.0 to accept only those factors which explained more of the variation than would a single variable. Varimax rotation was used to more clearly differentiate among the factors. I included all of the continuous variables in an initial PCA on both females and pups, but found that the large numbers of missing values in HI, FMP and FMR caused a reduction in the sample size available for the analysis. Therefore, I calculated two sets of PCA; one including the three variables, to examine their general contribution to the variability, and one without, to be more confident of the relationships described by the procedure. The relationship between SHAPE and NPARTS was assessed using Kruskal-Wallis tests (Monte-Carlo; 5000 replications).

To examine intra-individual variation, coefficients of variation (CV = standard deviation / mean) were calculated for each acoustic structure per individual. I then plotted these values on variability profiles, which represent a visual display of CVs for each acoustic variable and are not meant to imply continuity between the variables. The contours of each profile may be visually compared to explore differences in the level of variation between the groups (Sokal and Braumann 1980; see also Insley 1992, Fig. 5). Wilcoxon signed-ranks tests were used to determine whether females and pups differed in coefficients of variation.

I used a one-way random effects (Model II) ANOVA on each acoustic structure to examine absolute differences in structures among individuals for both females and pups. Variation between individuals was explored by calculating the added variance component (s^2_A) among groups, which when expressed as a ratio with the total variance ($s^2_A/(s^2_A+s^2)*100\%$), provides an indication of the inter-individual variation in the sample (Sokal and Rohlf 1981). I plotted the values of s^2_A on variability profiles. Although these were not used by Sokal and Braumann (1980) or Insley (1992), they may serve the purpose of enabling visual comparisons both between groups and between CV and s^2_A. I used Wilcoxon signed ranks tests to test for differences in s^2_A between females and pups. Likelihood ratio tests were used to assess the dependence of SHAPE on individuality.

As a further test of individuality, I used discriminant function analysis (DFA) which attempts to explain the variation between each individual by assigning calls to individuals based on similarities among the acoustic variables. Since the results of DFA are dependent on sample size, two females (XX68 and XX98) were randomly selected and excluded from this analysis, to enable comparisons between a sample of 13 females and 13 pups. DFA is also sensitive to missing values, so the variables HI, FMP and FMR were excluded from the analysis. For both females and pups, I used a stepwise DFA with minimization of Wilk's λ ($F_{IN} = 3.84$; $F_{OUT} = 2.71$) as the selection criterion for variables to be included in a function.

To verify the validity of the discriminant functions, I ran a cross-validation procedure as suggested by Smith *et al.* (1982). I randomly split the data into two groups of approximately equal size, then used one group to derive the discriminant functions, as before. The remaining 50% of the data were then subjected to classification tests using the new functions, and the rates of classification were compared to those obtained for the entire data set using Wilcoxon signed-rank tests.

6.3 RESULTS

Descriptive statistics of acoustic variables and representative spectrograms for each individual are summarized in Appendix F.

6.3.1 Description of calls

Female calls

Calls given by female South American fur seals are high-pitched cries, typically composed of a guttural region followed by a loud tonal region in which the frequency peaks and then falls toward the end of the call (Figure 6-2a). At a broad scale, the SHAPE of female calls was most often Tonal+Pulsed (Figure 6-3). Among the 15 females sampled in this study, many females made tonal calls with little or no frequency modulation, approaching a pure monotone and resembling a soft wail (Figure 6-2b). Others made strongly frequency modulated calls that resembled trills (Figure 6-2c). One female consistently made entirely pulsed calls which sounded like a cow's "moo" (Figure 6-2d).

In general, female calls were long, approaching 1000 msec in duration and consisting of two to three parts (Table 6-1). The number of parts in a call was dependent on its SHAPE (Kruskal-Wallis U = 78.80, df = 4, $p < 0.001$); predictably, calls consisting of only pulsing or tonal regions contained fewer parts, but calls that had a SHAPE of Tonal+Pulsed were most often 2- or 3-part calls. The fundamental frequency typically varied from 800 - 1000 Hz within a call, with the greatest energy in this range. Energy peaks appeared to occur at each harmonic, decreasing in intensity as the frequency increased (Table 6-1).

Pup calls

South American fur seal pups emit high energy calls which sound to the human ear like a lamb's bleat. Pup calls are often completely pulsed or a complex combination of pulsed and tonal elements (Figure 6-3, Figure 6-4a). Many pups make staccato calls, consisting of many pulses made in succession (Figure 6-4b). FM is also common in pup calls, resulting in a squeal-like sound (Figure 6-4c). One pup's calls were very similar to the two-part structure of adult females (Figure 6-4d). Purely tonal calls were rare in pups (Figure 6-3).

Pup calls were generally less than 1000 msec long (Table 6-1). The number of parts per call varied substantially, and was dependent on the SHAPE of the call (Kruskal-Wallis U = 104.94, df = 4, $p < 0.001$). As for females, Tonal+Pulsed calls were usually 2- or 3-parts. Exclusively pulsed calls were the most variable, ranging from simple 1-part bleats to 15-part staccato calls. Pup calls were higher frequency than those of females, with harmonic intervals around 1000 Hz (Table 6-1). Calls with harmonic intervals of less than 500 Hz were generally perceived as pulsed. Although the range of each energy peak overlapped substantially, peaks tended to occur at approximately 1400, 2800 and 4200 Hz, and the lowest visible harmonic appeared to coincide with the lowest energy peak (Table 6-1). In pups, AMP2 and AMP3 were more likely to exceed 100% than in females, indicating that the higher frequency ranges were more often amplitude-emphasized (see Figure 6-4a).

6.3.2 Dimensionality of call variation

Both female and pup calls are variable in at least three acoustical dimensions. The principal components analyses extracted three factors for female calls and four for pup calls, that explained over 75% of the variance in the sample (Tables 6-2, 6-3).

For female calls, variables describing frequency characteristics loaded highest on the first factor, and accounted for approximately 40% of the variation (Table 6-2a). The amplitude variables, AMP2 and AMP3, were strongly correlated with the second factor, and add another level of dimensionality that explains a further 16.4% of the variation. Call duration (DUR) and the number of parts (NPARTS) loaded on the third factor, but with opposite signs, suggesting that longer calls have fewer parts within their acoustic structure.

Although sample sizes were low, the PCA that included all of the variables revealed further patterns (Table 6-2b). The harmonic interval of the call (HI) only helped explain a further 4.6% of the variance explained by Factor 1 (44.1% - 39.5%, from Table 6-2). With the inclusion of the variables describing frequency modulation (FMP and FMR), a fourth factor was extracted that included only the variable NPARTS. Thus, frequency modulation likely contributes additional variation to the structure of female calls.

Compared to those of females, pup calls were variable in more dimensions, and the acoustic structures contributed to the variation in different ways (Table 6-3a). In the PCA that excluded HI, FMP and FMR, almost 30% of the variation was attributed to the characteristics of the lowest visible harmonic, while the variables describing higher ranges of emphasized frequencies (PEAK2 and PEAK3) explained a further 20%. As in females, AMP2 and AMP3, and DUR and NPARTS, loaded on separate factors which explained about 17% and 12% of the variation, respectively.

When the variables HI, FMP and FMR were included, the frequency of the lowest frequency peak (PEAK1) was associated with the other PEAK variables instead of with variables describing the first harmonic (Table 6-3b). The period of the frequency modulation (FMP) loaded on the same factor as duration and number of parts, perhaps because the latter variables also describe a temporal characteristic of the calls. All of these variables loaded with the same sign, indicating that for pups, longer calls tend to have more parts and longer periods of FM. Finally, the fifth factor, containing FMR and HI, accounted for only 8.4% of the variation in the sample. Unlike female calls, the harmonic interval of pup calls was not associated with ENDF, MAXF or INF. However, these relationships can only be generalized because of the low sample sizes used in this analysis.

6.3.3 Individual variation

The calls of both females and pups show substantially more variation between individuals than within. Coefficients of variation (CV) within individuals were relatively low for both classes, with the exception of the variables describing FM (Figure 6-5a). Female calls had lower CVs, indicating a greater tendency towards stereotypy, and the difference between CVs of females and pups for a particular acoustic structure approached significance (Wilcoxon signed-ranks test, $Z = -1.92$; $n = 13$; $p = 0.055$). In contrast, added variance components (s^2_A), which describe the variation among groups, were more variable but generally much higher than CVs (Figure 6-5b). Overall, the s^2_A of female calls was significantly higher than that of pup calls for a given acoustic structure (Wilcoxon signed-ranks test, $Z = -2.20$; $n = 13$; $p = 0.03$), indicating that calls are more variable among females than among pups. Comparisons of the absolute differences within call structures among individuals were statistically significant for all acoustic variables, for both females and pups (Table 6-4).

The discriminant function analysis showed that calls of both females and pups could be distinguished based on linear combinations of acoustic structures about 60 to 70% of the time (Table 6-5). These classification rates are conservative, because the variables HI, FMP and FMR were excluded from the DFA.

For females, calls were correctly assigned to individuals about 70% of the time, although some females' calls were much more distinguishable than others (Table 6-5a). Calls of females XX54, XX80 and N410 had low classification rates, although these were still much higher than chance (i.e. for 13 females, 1/13 = 7.7%). The variables PEAK1 - PEAK3 were not extracted by the DFA. The remaining variables were distributed among seven functions, the first two of which explained almost 65% of the variation between females (Table 6-6a). MAXF ($R = 0.85$) and NPARTS ($R = 0.71$) were most strongly correlated with the first and second functions, respectively. These results suggest that in the absence of HI, FMP and FMR, the statistical procedure discriminated the calls on the basis of the number of parts per call and the maximum frequency of the lowest visible harmonic.

The DFA was less successful at assigning calls to pups, averaging about 60% correct classification (Table 6-5b). Calls of four pups (N417, XX71, XX99, N433) appeared to show low individuality. However, the distribution of mis-classified calls did not seem random. For example, seven of N433's calls were classified to N417, and five of XX71's calls were classified to XX27. In the first pair, the acoustic characteristics seem to differ only with respect to FMR and the presence of pulsing (see Appendix F). Both of these pups' calls are characterized by the presence of frequency modulation, so perhaps the exclusion of the variables FMP and FMR from the DFA resulted in the low classification rate for N433. In the second pair, calls of both XX71 and XX27 are typically stacatto, and the PEAK frequencies are very similar (see Appendix F). The DFA did not extract the variables INF, ENDF, PEAK1 or AMP2. The first two functions contributed to almost 65% of the variation among pups (Table 6-6b). As with female calls, NPARTS (R = 0.92) and MAXF (R = 0.62) were correlated with the first two functions, although NPARTS was associated with the first function and MAXF with the second, suggesting that pup calls were discriminated by the statistical procedure primarily on the basis of the number of parts per call.

Overall, the cross-validation tests had lower rates of classification than the DFA using the entire data set, although the classification rates were higher for three females and four pups. For females, classification rates ranged from 8.3% to 92.3% ($\bar{x}$ = 55.4%) and these were barely significantly different for each female compared to the original DFA (Wilcoxon signed-ranks test: Z = -2.03, p = 0.04). The classification rates for pups ranged from 0% (N433) to 83.3% ($\bar{x}$ = 51.4%); these were not significantly different for each pup (Wilcoxon signed-ranks test: Z = -1.85, p = 0.06). Also, the cross-validation DFA resulted in factor loadings and eigenvalues very similar to those of the original DFA. Thus, given the reduced sample size, the cross-validation tests seem to indicate that the original DFA were valid.

6.4 DISCUSSION

Vocal signals that are used as signatures must exhibit low variability within and relatively high variability among individuals. The vocalizations used between mother and pup South American fur seals at Punta San Juan, Peru, do appear to show acoustic stereotypy. Not only were calls individualistic, but discrimination between individuals was possible based on linear combinations of various acoustic variables. This study supports Trillmich and Majluf's (1981) suggestion that mothers and pups have individualistic calls. Additionally, it is consistent with research on other colonially breeding pinniped species, which have shown (based on experimentation) or suggested (based on field observations) that mothers and pups exhibit individualistic calls (Bartholomew 1959; Peterson and Bartholomew 1969; Stirling and Warneke 1971; Petrinovich 1974; Trillmich 1981; Takemura *et al.* 1983; Roux and Jouventin 1987; Insley 1989, 1992; Hanggi 1992).

The FACs and PACs of South American fur seals appear to be discriminated on the basis of a combination of frequency, temporal and amplitude-related characteristics. Frequency characteristics such as the harmonic interval (fundamental frequency) and the frequency of the lowest visible harmonic explained about 40% of the variability among calls of both females and pups (Tables 6-2, 6-3). This is consistent with studies of other mammalian species, in which characteristics of the fundamental frequency were reported to be the best markers for individuality (e.g. Lenhardt 1977; Smith *et al.* 1982; Sieber 1986; Perry and Renouf 1988; Tooze *et al.* 1990; Scherrer and Wilkinson 1993). In addition, relatively high frequency calls with harmonic structure and frequency modulation are highly directional (Marler 1955). Therefore, the calls made by mother and pup South American fur seals might also facilitate location of the calling individual.

The calls of adult females were most often tonal with a rich harmonic structure, and the bands of energy-emphasized frequency ranges (PEAK1 - PEAK3) typically coincided with the harmonics (Table 6-2a, Figure 6-2). In contrast, pup calls were typically more pulsed than those of females, and the peak frequency bands did not appear to be related to the harmonic structure of the call (Table 6-3a, Figure 6-4). These bands may represent formant frequencies that result from supralaryngeal modification of the sound produced by the vocal cords. Thus, because they are directly related to the anatomy of each animal, it is not surprising that they might contribute to the individuality of pup calls. If this is so, then maturational changes in pups' vocal anatomy might change the acoustic characteristics of their calls. However, Insley (1996) found that northern fur seal mothers responded to both old and recently-recorded calls of their own pups, so changes in formant frequencies may not affect the overall individuality of calls.

Temporal features such as call duration and the number of distinguishable parts per call also appeared to play a role in discrimination between individuals, particularly in pups. This also appears to be the case for northern fur seal and northern elephant seal (*Mirounga angustirostris*) vocalizations (Insley 1992). Other studies have suggested that calls that consist of many brief sounds repeated in sequence may aid in localizing the sender (Marler 1955; Balcombe and McCracken 1992). By exhibiting variation in the number of call parts, South American fur seal pups may provide mothers with cues to both identification and location.

Pups tended to have more complex calls than females, with a tendency toward repetitive pulsing (e.g. Figure 6-4b). Miller and Murray (1995) suggest that variation of the number of parts in a call represents a level of syntactic complexity that is required in species breeding in high densities. By comparison, calls of solitary breeding phocid pups tend to be brief and composed of few parts (Renouf 1984; Perry and Renouf 1988; Job *et al.* 1995). Harp seal (*Phoca groenlandica*) pups were found to produce complex calls, although these were not individualistic and Miller and Murray (1995) attributed the complexity to the early use of sounds which will be used in complex underwater sound production as adults, as other mammal and bird infants produce “nonsense sounds” or warbles (for reviews of vocal learning see Nottebohm 1972; Ehret 1980; Kroodsma and Miller 1982; Janik and Slater 1997).

In this study, calls were correctly assigned to individuals about 60 to 70% of the time (Table 6-5), based on the acoustic variables that were measured. Comparable studies of other mammal species have reported similar or higher rates of classification (e.g. 88 - 100% for squirrel monkeys, *Saimiri sciureus* (Smith *et al.* 1982); 60% for Mexican free-tailed bats (Gelfand and McCraken 1986); 50 - 100% for ringtailed lemurs, *Lemur catta* (Macedonia 1986); 72 - 100 % for timber wolves, *Canis lupus* (Tooze *et al.* 1990)). In all of these studies, however, classification rates were significantly higher than the prior probability of correctly classifying the calls based on random chance. That the classification rates were not higher overall may be explained by a number of factors. First, it is not known which acoustic features the animals themselves use as cues to discriminate among individuals. Mother and pup fur seals may recognize the sound pattern resulting from a combination of acoustic structures, rather than the absolute values of the structures themselves (e.g. Scherrer and Wilkinson 1993). Furthermore, recognition may occur at two levels: discrimination of "familiar" from "strange" (recognition of one individual but not of others), and discrimination among individuals, which is common in social groups comprised of related individuals (Beecher 1982). Although Hanggi and Schusterman (1990) have suggested that kin affiliation may occur in otariids, there is no evidence that wild otariids recognize or associate with animals outside of the mother-pup relationship. Thus, calls of mothers and pups may not need to be individualistic compared to every other animal in the colony, but exhibit sufficient stereotypy that with a combination of other cues (geographical, visual and olfactory; see Chapter 5), mothers might only be required to distinguish their pups (and vice versa) from a small area of the breeding colony.

Calls of female South American fur seals were more individualistic than those of pups. Mothers that have easily distinguishable calls can be recognized from a distance, which is beneficial to pups by reducing the risk of approaching unrelated females. Because mothers ultimately seem to recognize their pups based on olfactory cues (Chapter 5), the selective pressures on call stereotypy may not be as high for pups as for females. Alternatively, pup calls may be more variable due to the developmental state of the vocal anatomy. The calls of northern fur seal pups appear to change gradually over the first few months (Insley 1996). Although I detected no age effect in the pups in my study (Appendix C), I was limited to pups between the age of 8 to 36 days.

In summary, the calls of mother and pup South American fur seals appear to exhibit sufficient stereotypy that recognition and discrimination among individuals is possible. The acoustic analysis does not prove that the calls are actually used for recognition, but observations of searching and reunion behaviour between mothers and pups (Chapter 5) suggest that vocal cues are important for recognition, and that pups are able to recognize mothers based on their calls.

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Table 6-1. Summary of acoustic variables measured from calls of 15 females and 13 pups. All values are in Hz except NPARTS (n), DUR and FMP (msec) and AMP (%).

	Females				Pups			
	Mean	S.E.	Range	N	Mean	S.E.	Range	N
DUR	1057	19.0	361 - 2231	300	600	13.9	181 - 1262	260
NPARTS	2.7	0.07	1 - 7	300	4.7	0.18	1 - 15	260
HI	905	11.4	530 - 1660	271	1030	18.5	410 - 1440	157
INF	728	6.7	500 - 1310	298	1182	15.0	590 - 2000	258
MAXF	944	11.2	560 - 1660	300	1470	21.3	750 - 2630	260
ENDF	791	7.5	530 - 1380	300	1253	18.7	590 - 2190	258
PEAK1	871	9.7	580 - 1510	300	1364	12.9	850 - 2260	260
PEAK2	1733	19.9	1040 - 3580	298	2824	31.5	1450 - 4510	260
PEAK3	2721	36.9	1590 - 5870	278	4143	45.3	2960 - 6080	249
AMP2	81	0.8	46 - 141	298	86	0.8	50 - 130	260
AMP3	71	0.8	45 - 123	278	83	1.0	46 - 173	249
FMP	31	1.7	9 - 72	69	42	1.8	14 - 98	87
FMR	353	27.6	90 - 1030	69	327	18.6	60 - 840	87

Table 6-2. Summary of PCA on acoustic variables for female fur seal calls, showing rotated factor loadings of each variable on the factors having an eigenvalue > 1.0. Variables that loaded highest on each factor are indicated with bold type.

a) HI, FMP and FMR excluded (N = 276)

Acoustic structure	Factor 1	Factor 2	Factor 3
MAXF	**0.901**	-0.096	0.147
PEAK1	**0.889**	-0.051	0.060
PEAK2	**0.882**	-0.096	0.106
PEAK3	**0.727**	-0.199	0.054
ENDF	**0.690**	-0.079	0.031
AMP3	-0.555	**0.923**	-0.018
AMP2	-0.093	**0.892**	-0.063
INF	0.367	-0.432	0.075
DUR	0.003	0.021	**-0.826**
NPARTS	0.186	-0.079	**0.711**
Eigenvalue	3.948	1.638	1.126
Variance explained	39.5%	16.4%	11.3%
Cumulative variance	39.5%	55.9%	67.1%

b) All acoustic variables (N = 67)

Acoustic structure	Factor 1	Factor 2	Factor 3	Factor 4
PEAK2	**0.884**	0.116	0.024	0.258
PEAK1	**0.881**	0.234	-0.076	-0.041
HI	**0.867**	0.310	-0.060	-0.232
MAXF	**0.827**	0.420	-0.072	-0.147
RESF3	**0.797**	-0.037	-0.134	0.385
INF	**0.575**	0.243	-0.294	0.253
ENDF	0.218	**0.800**	-0.205	-0.022
FMR	0.185	**0.779**	-0.238	0.192
FMP	0.097	**0.714**	0.042	0.037
DUR	-0.345	**-0.613**	0.186	-0.208
AMP3	-0.103	-0.066	**0.951**	-0.031
AMP2	-0.080	-0.267	**0.892**	-0.091
NPARTS	0.073	0.193	-0.085	**0.920**
Eigenvalue	5.728	1.947	1.294	1.124
Variance explained	44.1%	15.0%	10.0%	8.6%
Cumulative variance	44.1%	59.0%	69.0%	77.6%

Table 6-3. Summary of PCA on acoustic variables for fur seal pup calls, showing rotated factor loadings of each variable on the factors having an eigenvalue > 1.0. Variables that loaded highest on each factor are indicated with bold type.

a) HI, FMP and FMR excluded (N = 245)

Acoustic structure	Factor 1	Factor 2	Factor 3	Factor 4
MAXF	**0.912**	0.024	0.037	-0.033
ENDF	**0.899**	0.000	-0.124	0.064
INF	**0.822**	0.050	0.102	0.181
PEAK1	**0.567**	0.406	0.174	-0.936
PEAK2	0.161	**0.921**	-0.044	0.016
PEAK3	-0.024	**0.888**	-0.201	0.007
AMP2	0.087	0.036	**0.913**	-0.066
AMP3	-0.011	-0.288	**0.883**	-0.077
DUR	-0.064	0.017	-0.022	**0.893**
NPARTS	0.187	-0.013	-0.116	**0.865**
Eigenvalue	2.949	2.147	1.678	1.179
Variance explained	29.5%	21.5%	16.8%	11.8%
Cumulative variance	29.5%	51.0%	67.7%	79.5%

b) All acoustic variables (N = 82)

Acoustic structure	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
ENDF	**0.903**	0.023	-0.125	-0.002	0.139
MAXF	**0.902**	0.140	0.031	0.111	0.159
INF	**0.855**	0.150	0.155	-0.004	0.014
PEAK2	0.125	**0.926**	-0.121	-0.014	-0.036
PEAK3	-0.023	**0.917**	-0.174	-0.048	0.049
PEAK1	0.393	**0.715**	0.192	-0.080	-0.114
AMP2	0.017	0.091	**0.917**	-0.028	-0.061
AMP3	0.045	-0.344	**0.847**	-0.131	0.086
DUR	0.087	-0.052	-0.150	**0.808**	-0.062
NPARTS	0.123	-0.053	0.090	**0.697**	0.058
FMP	-0.179	0.015	-0.112	**0.649**	0.255
FMR	0.271	0.194	-0.095	0.050	**0.817**
HI	0.034	-0.246	0.097	0.143	**0.770**
Eigenvalue	3.294	2.317	2.024	1.191	1.090
Variance explained	25.3%	17.8%	15.6%	9.2%	8.4%
Cumulative variance	25.3%	43.2%	58.7%	67.9%	76.3%

Table 6-4. Results of analyses of variance among individuals of acoustic features of South American fur seal female and pup vocalizations. All tests are significant at $p < 0.001$.

	Females		Pups	
Structure	df	F	df	F
DUR	14, 285	16.86	12, 247	16.62
NPARTS	14, 285	20.24	12, 247	46.55
HI	13, 257	37.65	8, 148	22.56
INF	14, 283	13.65	12, 245	12.43
MAXF	14, 285	48.84	12, 247	21.12
ENDF	14, 285	19.73	12, 245	15.77
PEAK1	14, 285	36.74	12, 247	9.12
PEAK2	14, 283	20.87	12, 247	9.81
PEAK3	14, 263	10.28	12, 236	12.91
AMP2	14, 283	13.67	12, 247	5.24
AMP3	14, 263	14.13	12, 236	13.97
FMP	5, 55	6.87	5, 81	6.37
FMR	5, 55	18.35	5, 80	6.53

Table 6-5. Classification of calls to individual South American fur seals based on the discriminant function analysis, arranged in descending order of classification rate (%). The number of calls assigned correctly is indicated in bold type.

a) Adult females

			Female to which calls were assigned												
Female	n	%	XX58	XX77	XX26F	N442	X72	XX70	N412	N418	N408	N434	XX54	XX80	N410
XX58	20	95.0	**19**	-	-	-	-	-	-	-	-	-	-	-	1
XX77	20	95.0	-	**19**	-	-	-	-	-	-	-	-	-	-	1
XX26F	20	94.7	-	-	**18**	-	-	-	-	-	-	-	-	-	1
N442	20	82.4	-	-	1	**14**	-	2	-	-	-	-	-	-	-
X72	19	75.0	-	-	1	-	**15**	-	-	1	-	1	-	2	-
XX70	19	75.0	-	-	-	3	1	**15**	-	-	-	-	1	-	-
N412	17	58.8	1	1	-	-	1	-	**10**	-	1	-	1	-	2
N418	20	58.8	-	-	1	-	-	1	1	**11**	-	-	-	-	4
N408	14	57.1	-	1	-	1	-	-	3	-	**8**	-	-	1	-
N434	20	55.6	-	1	1	-	2	-	-	-	-	**10**	-	4	-
XX54	20	50.0	-	-	-	-	3	-	3	3	-	1	**10**	-	-
XX80	20	45.0	-	-	-	-	2	1	-	2	3	3	-	**9**	-
N410	20	36.8	1	2	2	1	-	-	3	2	-	1	-	2	**7**
N, $\bar{x}$	242	68.2													

Table 6-5. Classification of calls to individual South American fur seals based on the discriminant function analysis, arranged in descending order of classification rate (%). The number of calls assigned correctly is indicated in bold type.

b) Pups

			Pup to which calls were assigned												
Pup	n	%	N415	N409	N407	XX26	XX27	XX69	XX75	N403	XX73	N417	XX71	XX99	N433
N415	20	85.0	**17**	-	-	-	-	-	-	-	-	-	1	2	-
N409	17	82.4	-	**14**	-	-	-	1	1	-	-	-	-	1	-
N407	20	80.0	-	-	**16**	-	2	1	-	-	1	-	-	-	-
XX26	19	78.9	-	-	-	**15**	-	-	1	-	-	1	2	-	-
XX27	20	70.0	-	-	2	-	**14**	-	-	-	2	-	2	-	-
XX69	20	70.0	-	-	1	-	-	**14**	-	-	5	-	-	-	-
XX75	20	65.0	2	1	-	-	-	-	**13**	-	-	2	1	1	-
N403	14	64.3	3	-	-	-	-	-	1	**9**	1	-	-	-	-
XX73	19	63.2	-	-	-	-	3	3	-	-	**12**	-	-	1	-
N417	20	45.0	-	-	-	1	-	-	5	-	1	**9**	1	-	3
XX71	20	40.0	-	-	-	1	5	-	1	-	1	3	**8**	1	-
XX99	20	30.0	3	-	-	2	-	-	1	2	1	1	4	**6**	-
N433	20	15.0	1	-	-	1	1	-	-	3	-	7	2	2	**3**
N, x̄	249	60.2													

Table 6-6. Results of the discriminant function analysis on South American fur seal calls.

a) Adult females

Function	Eigenvalue	Variance explained (%)	Cumulative variance (%)	Canonical correlation
1	3.105	44.9	44.9	0.87
2	1.384	20.0	64.9	0.76
3	0.892	12.9	77.7	0.69
4	0.649	9.38	87.1	0.63
5	0.529	7.6	94.8	0.59
6	0.260	3.8	98.52	0.45
7	0.103	1.5	100.0	0.31

Wilk's $\lambda = 0.02$; Chi-square = 963.75; df = 84; $p < 0.001$

b) Pups

Function	Eigenvalue	Variance explained (%)	Cumulative variance (%)	Canonical correlation
1	2.634	43.2	43.2	0.85
2	1.496	24.6	67.8	0.77
3	0.779	12.8	80.5	0.66
4	0.652	10.7	91.2	0.63
5	0.339	5.6	96.8	0.50
6	0.120	3.2	100.0	0.41

Wilk's $\lambda = 0.02$; Chi-square = 880.31; df = 72; $p < 0.001$

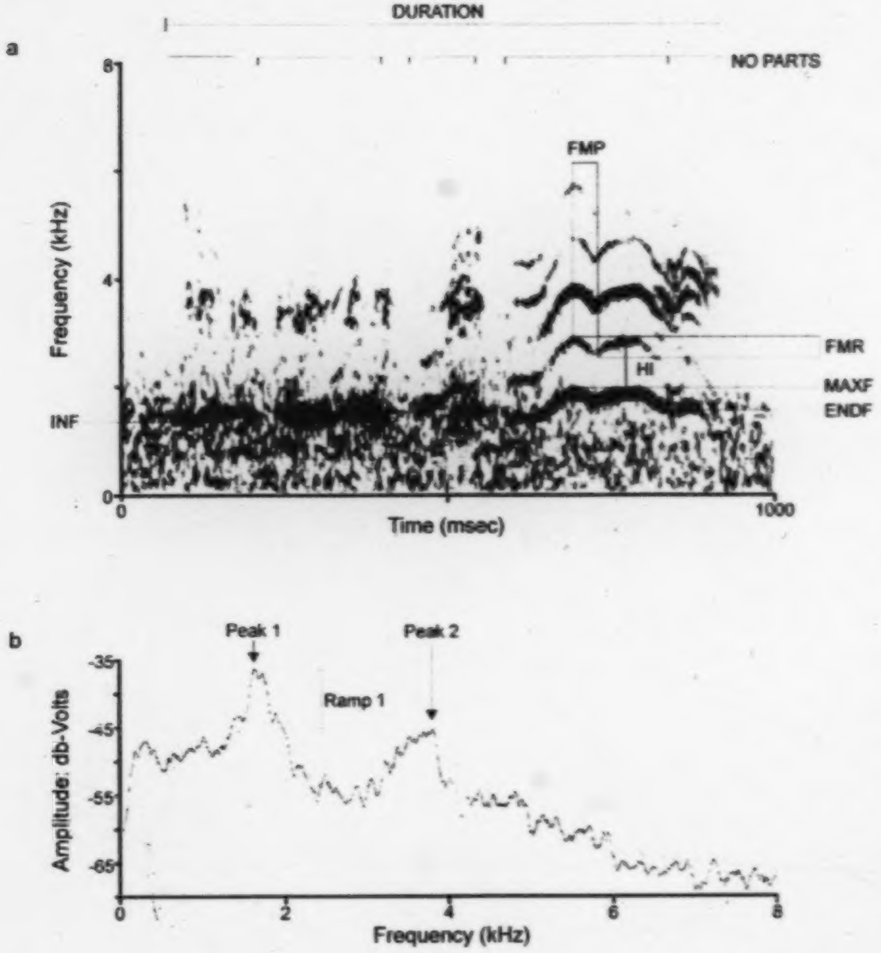

Figure 6-1. Digital representations of a pup's call showing acoustic features measured in this study. a) spectrogram (frequency bandwidth = 39 Hz); b) power spectrum.

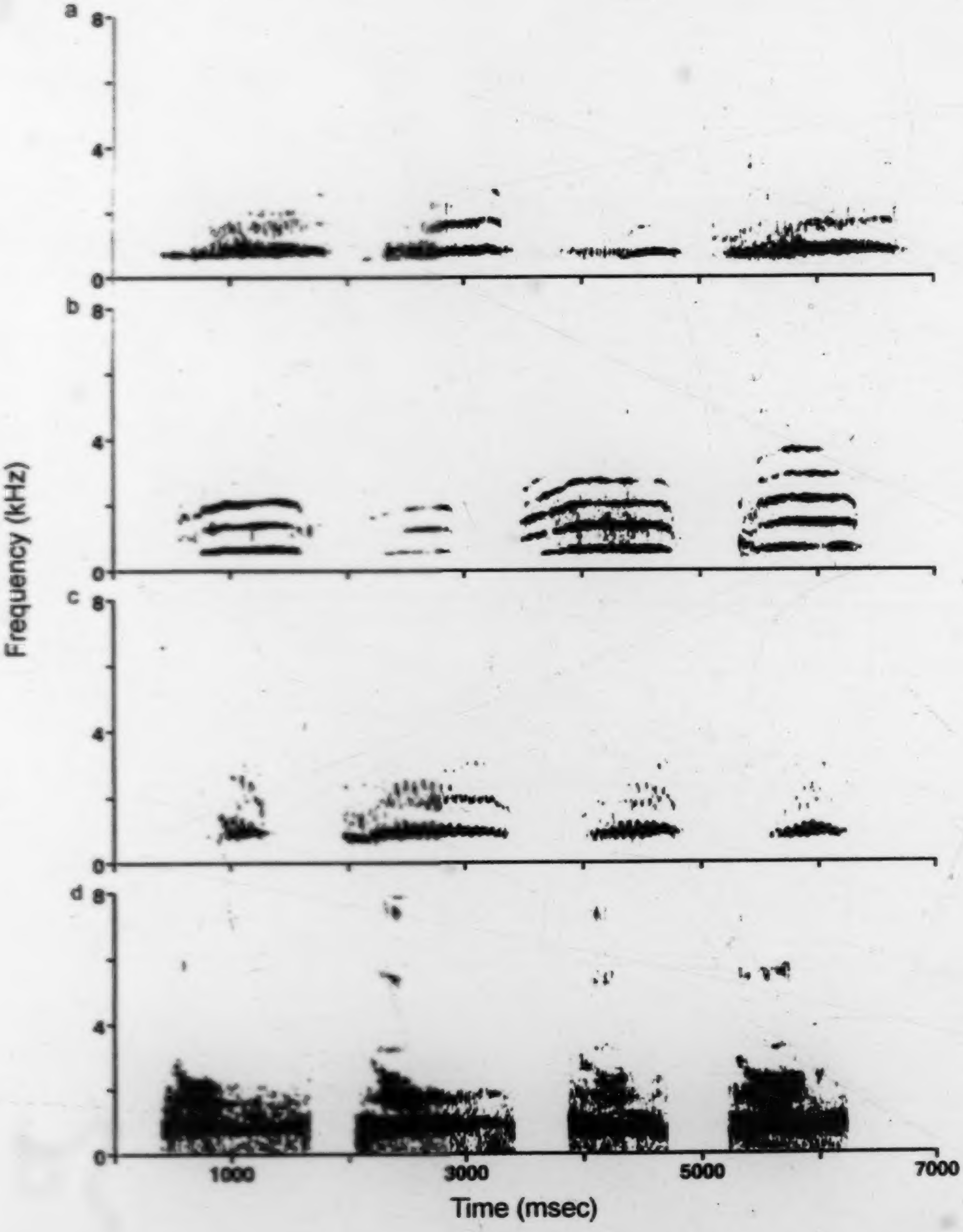

Figure 6-2. Representative spectrograms of calls made by four female fur seals, showing inter- and intra-individual variation. a) Tonal+Pulsed call (N434); b) Tonal call (XX70); c) Frequency modulated call (XX77); d) Completely pulsed call (N442). Frequency bandwidth of spectrograms = 39 Hz.

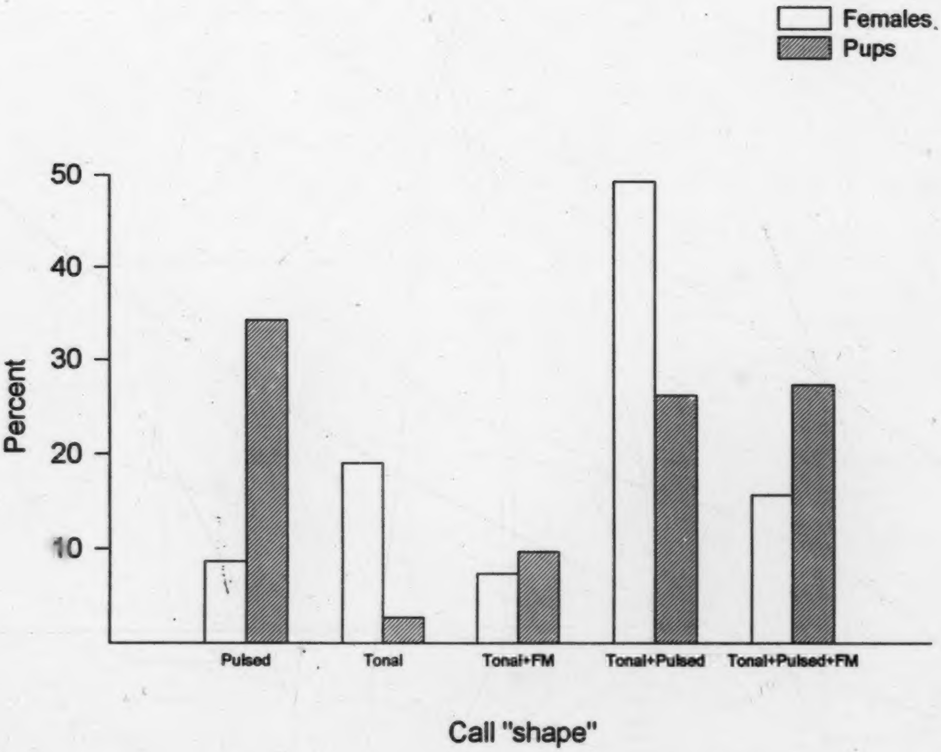

Figure 6-3. Distribution (%) of the types of calls given by mother and pup South American fur seals, arranged by the variable "SHAPE".

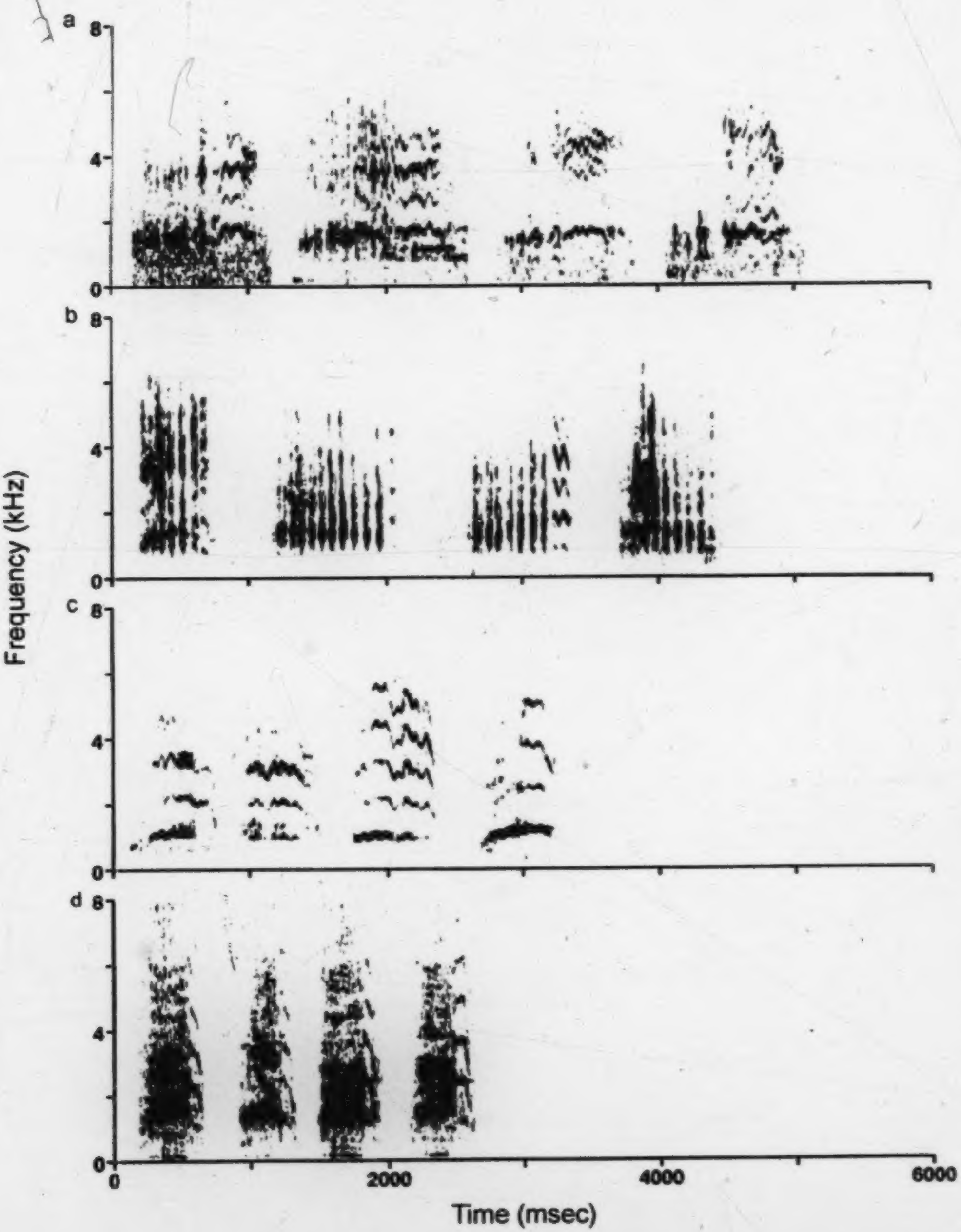

Figure 6-4. Representative spectrograms (vertical axes in kHz) of calls made by four fur seal pups, showing inter- and intra-individual variation. a) Complex Tonal+Pulsed call (N403); b) Staccato call (XX27); c) Frequency modulated call (N417); d) Tonal+Pulsed call (XX26). Frequency bandwidth of spectrograms = 39 Hz.

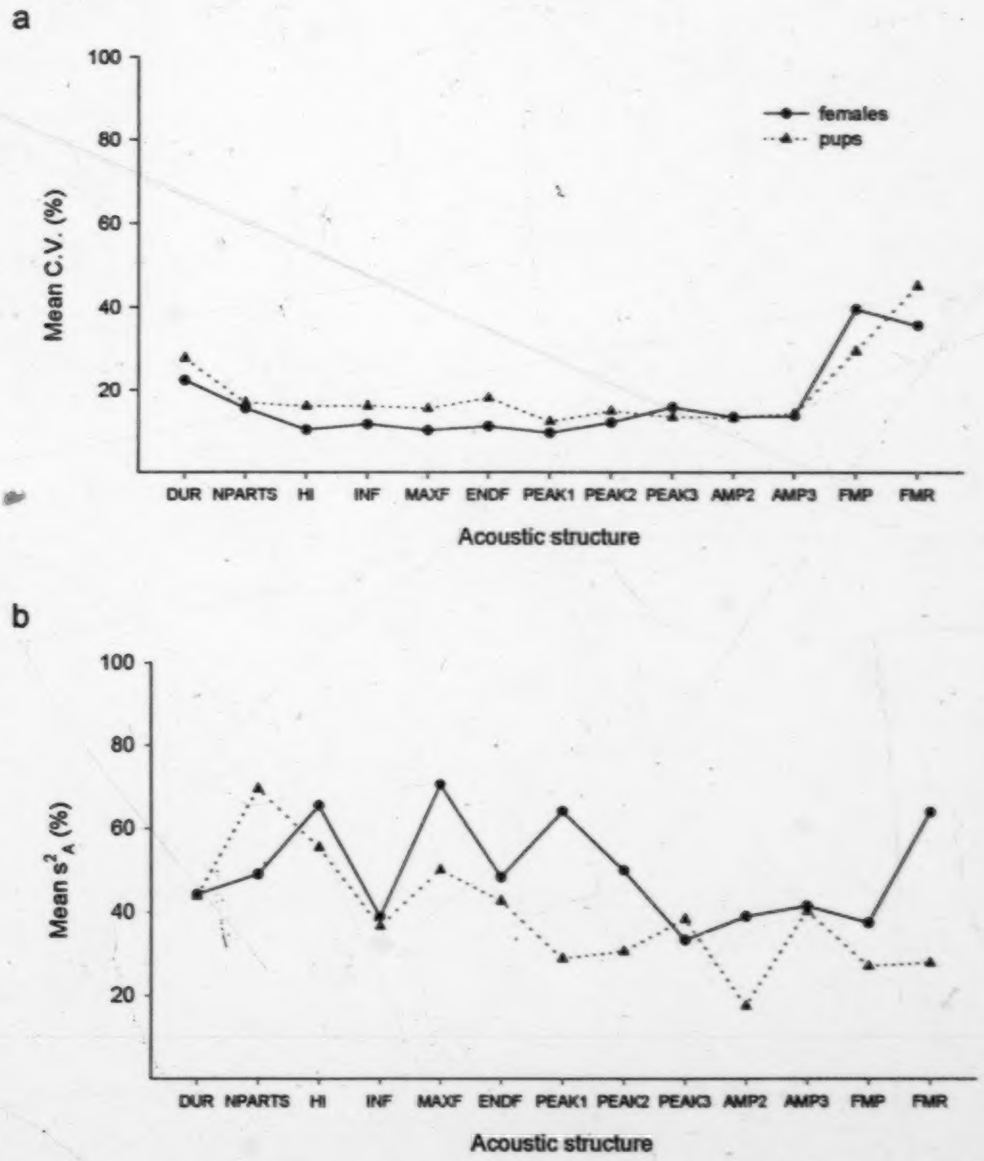

Figure 6-5. Variability profiles showing a) within-individual variation and b) between-individual variation of acoustic structures in calls of female and pup South American fur seals.

7. MECHANISMS FOR MOTHER-PUP RECOGNITION BY VOCAL CUES IN SOUTH AMERICAN FUR SEALS.

7.1 INTRODUCTION

In many colonially breeding species, the potential exists for parents to confuse their own offspring with others, since immature animals that rely on provisioning by one or both parents are typically left in large groups of unrelated individuals while their parents forage. For species in which parents invest heavily in their offspring, mechanisms for individual recognition of offspring by parents would minimize the chance of misdirecting parental investment (Trivers 1972; for reviews see Colgan 1983; Holmes and Sherman 1983; Hepper 1986; Porter 1987; Waldman 1988; Holmes 1990; Clutton-Brock 1991).

The ability of parents to recognize their young relies, in part, on offspring having distinct "signatures" with greater inter- than intra-individual variation (Beecher 1982). Such signals must provide specific information about the identity of the sender and be repeatable (Boake 1989). Although visual and olfactory cues may enhance offspring signatures, vocalizations are typically the major component among colonial species because acoustic cues are the most efficient over long distances (Holmes 1990; Miller 1991).

Parents may recognize their offspring by one of two mechanisms. If signature calls are heritable or if infants are selected to imitate the signature calls of their parents, then recognition may occur through "phenotypic matching" whereby parents compare their calls to those of potential offspring and only accept individuals whose call matches their own (Beecher 1982). Signature similarities between parents and infants have been suggested in some species of birds and mammals, including ancient murrelets (*Synthliboramphus antiguus,* Jones *et al.* 1987), spider monkeys (*Ateles geoffroyi*, Chapman and Weary 1990), evening bats (*Nycticeius humeralis,* Scherrer and Wilkinson 1993), and bottlenose dolphins (*Tursiops truncatus*, Sayigh *et al.* 1995). It is difficult to distinguish whether young of these species acquire their signatures by genetic inheritance or by imitation of their parents. In most species, the latter seems more likely, since mimicry of parental signatures has the advantage that a signal acquired this way may be continuously compared against its template (Beecher 1982; Falls 1982). However, Scherrer and Wilkinson (1993) note that in species such as evening bats in which intermingling of young occurs directly after birth, infant calls must be inherited from the parents since there would be no time for learning to occur.

Beecher (1982) described an alternative mechanism for kin recognition, in which an offspring's call need not be heritable or copied from the parent. Parents may learn the signature call of their offspring while there is reliable contextual evidence of relatedness (for example, proximity), and later locate their offspring based on these learned cues. In such cases, the offspring signatures must provide enough information about individual identity for recognition to be possible, but phenotypic matching need not occur (Beecher 1982). For example, in bank swallows (*Riparia riparia*) and cliff swallows (*Hirundo pyrrhonota*), intra-specific cross-fostering and playback experiments have shown that adult swallows learn the signatures of foster chicks that are transferred to their nests before the chicks' calls stabilize as signatures (Beecher *et al.* 1981, 1986).

Fur seals and sea lions (Pinnipedia: Otariidae) are characterized by colonial breeding in dense aggregations. Individuality of offspring calls and efficient mother-pup recognition have been documented for several species (Trillmich 1981; Takemura *et al.* 1983; Roux and Jouventin 1987; Insley 1992; see also Chapters 5 and 6). However, the mechanisms by which pups acquire their individual calls and mothers recognize these have not yet been investigated. Do mother otariids learn their pups' calls, or do they recognize their pup on the basis of similarity to their own calls? To examine whether recognition of pup calls results from phenotypic matching or from learning the calls of pups, I analyzed calls of known mother-pup pairs of South American fur seal (*Arctocephalus australis*). If recognition occurs via phenotypic matching, pup calls should share structural features with calls of their mothers. Furthermore, pups born to the same female in subsequent years (half-siblings) should also share similar call characteristics.

7.2 MATERIALS AND METHODS

See Chapter 6 for a description of recording and acoustic analysis. For this study, I used 20 calls from each of the 10 mother-pup pairs that were analyzed in Chapter 6. The variables FMP and FMR were not used in this analysis because of the large proportion of missing values.

I used several approaches to compare call structure between mothers and pups. First, to examine absolute differences in call characteristics, I employed one-way Model II ANOVA for each variable, within each mother-pup pair. Because call characteristics may differ in absolute values but still be related to one another, I used linear regression analysis to explore structural relationships between the calls of mothers and pups.

Finally, I used discriminant function analysis (DFA) to determine whether calls of pups could be assigned to their mothers, based on linear combinations of the acoustic variables. I used a modification of a DFA cross-validation procedure (see Chapter 6), in which the ten mothers were used to derive the discriminant functions, using a stepwise DFA with minimization of Wilk's λ ($F_{IN} = 3.84$; $F_{OUT} = 2.71$) as the selection criteria for variables to be included in a function. Because DFA is sensitive to missing values, the variables HI, FMP and FMR were excluded from the analysis. I then subjected the pup data to classification tests using the functions calculated from the mother data. In this procedure, pups should be classified to their mothers if their acoustic structure is similar.

I visually compared spectrograms of single calls from four pairs of half-siblings (pups born to the same mother in subsequent years). Because of time constraints and low sample sizes, I did not measure any acoustic features of these calls. Although inspecting the spectrograms may be subjective, I believe that there is sufficient individuality of pup calls that the spectrogram of a randomly-chosen call from each pup should be representative of the acoustic characteristics of an individual's calls.

7.3 RESULTS

Pup calls were not acoustically similar to those of their mothers (see Appendix F). Within each pair, the structure of a pup's call was different from that of its mother for most or all of the characteristics measured (Table 7-1), particularly for the variables describing frequency characteristics (HI - PEAK3) and duration. Among mother-pup pairs, there was no consistent pattern with which acoustic structures varied between mother and pup calls (Table 7-1).

Regression analysis revealed a strong positive relationship within call duration (Table 7-2, Figure 7-1). There were weaker, but still significant, negative relationships with the maximum frequency of the lowest harmonic (MAXF) and the lowest peak frequency (PEAK1) (Table 7-2, Figure 7-1). Most of the regressions described negative relationships, were greater than one or had relatively large standard errors, which might suggest that there was insufficient power in the tests to detect a significant effect between mothers and pups (Falconer 1981).

The discriminant functions derived from the characteristics of mothers' calls were unable to classify pups to mothers consistently (Table 7-3). A disproportionate number of pup calls were classified to females XX77 (134/191 = 70%) and N408 (44/191 = 23%). The only pup whose calls were correctly classified more than 12% of the time was that of XX77. However, the calls of this mother-pup pair differed with respect to every acoustic variable measured (Table 7-1). Therefore, the high classification rate of this pup is probably an artifact of the statistical procedure's tendency to assign pup calls to female XX77.

Inspection of the spectrograms of calls of half-siblings revealed no patterns of similarity between each pair of pups (Figure 7-2). In particular, the variables describing frequency and number of call parts, which were determined to contribute most to individuality of calls (Chapter 6), did not appear to be similar between half-siblings.

7.4 DISCUSSION

South American fur seal pups exhibit individually distinctive calls which their mothers use to locate and reunite with them on the crowded breeding beach. The range of call variation among pups is moderate to high (see Chapter 6). Within pairs of mothers and nursing pups, however, pup calls do not appear to share structural similarities with those of their mothers, nor did calls of half-siblings appear to resemble each other. These observations do not, however, eliminate the possibility that young fur seals' calls might converge upon those of their mothers later in their development.

Although the absolute values of call duration differed between mother and pup for all pairs tested (Table 7-1), there was a positive relationship (slope = 0.63, $r^2 = 0.67$) with respect to duration: mothers with long calls tended to have pups with long calls. Falconer (1981) states that when comparing characteristics of a parent to its offspring, the slope of the regression between the two individuals may be used to estimate heritability (h^2) of a trait. Numerous studies have used regression of acoustic or morphometric characteristics to estimate heritability (e.g. Boag and Grant 1978; Smith and Dhondt 1980; Boag 1983; Butlin and Hewitt 1986; Hedrick 1988; Scherrer and Wilkinson 1993). In this study, however, I believe that it is impossible to distinguish between genetic and environmental effects, particularly maternal influences. Thus, pups with longer calls may be genetically predisposed to produce long calls, or they may learn this behaviour from their mothers, especially since mothers' calls dominate the pups' acoustic environment for the first few days of life.

The regression analyses were unable to detect strongly significant relationships for any of the other variables, most likely due to the low sample size of ten mother-pup pairs. Falconer (1981:167) notes that estimation of h^2 based on 100 parent-offspring pairs would produce standard errors of about 0.2, so no estimates of h^2 under 0.4 would be significantly different from zero. Also, I analyzed each acoustic variable separately in this study, although earlier results (Chapter 6) showed that many of the variables were correlated and contributed to the same dimensions of variation. Boag (1983) and Butlin and Hewitt (1986) modified their analyses by regressing functions derived from principle components analysis (PCA) instead of individual variables. This was not practical in this study because the PCA functions differed between mothers and pups in the relative contribution of each variable (Chapter 6).

A disproportionate number of pup calls were classified to females XX77 and N408. One possible explanation for this result is that XX77's calls were typically shorter than most females and contained more parts, characteristics more like those of pup calls (See Appendix F). Although calls of both pups and adult females exhibit the greatest inter-individual variation in frequency-related characteristics (Chapter 6), the discriminant functions derived in Chapter 6 appeared to discriminate among pups on the basis of the number of call parts. Thus, the discriminant function analysis may have assigned more pup calls to that female on the basis of those two acoustic characteristics. Alternatively, the calls of XX77 (see Appendix F) were characteristically frequency modulated; indeed, this female was the only one in the sample whose calls were always tonal and always contained FM. Perhaps the DFA assigned most of the pup calls to XX77 simply because her calls were so different from those of most of the other females in the sample. Female XX77 may have been very young, since her weight at tagging was more like that of a sub-adult (P. Majluf unpubl. data). This may explain why her calls sounded more like those of juveniles.

The apparent lack of signal similarity between mothers and pups suggests that South American fur seals are unlikely to use phenotypic matching, so any recognition of pup calls probably stems from the mother learning the call. For the first seven to ten days after parturition, mothers and pups spend a large proportion of their time calling back and forth while close to each other (Chapter 3). Mothers most likely learn the characteristics of their pups' calls (and vice versa) during the post-natal attendance period, so that they are able to recognize their own pups when returning from their first foraging trip, a few days later. Pups may become familiar with their mothers' calls even before birth because mothers tend to vocalize frequently during the days immediately prior to parturition; if these sounds are audible to the fetus then they would be familiar to the neonate pup (Gould 1983). This might assist recognition between mothers and pups during the critical period in which the mother-pup bond begins to form.

The structure of pups' calls may change as pups mature (Appendix C), so mothers would need to continuously compare their pups' call to that stored in their memory, and update it when necessary. This process is thought to be relatively common among species which breed in high densities but in which infants do not intermingle immediately with unrelated young (e.g. gulls (Beer 1979), and several species of bats (Gelfand and McCracken 1986; Jones *et al.* 1991; Rasmuson and Barclay 1992)). Similarly, mother northern fur seals (*Callorhinus ursinus*) responded similarly to playbacks of recent (<1 week) and old (3-4 weeks) versions of their pup's call, suggesting that ontogenetic changes are compensated for as they occur (Insley 1996).

The mechanism by which pups acquire their signature calls remains unclear, although Beecher (1982) suggests that in species that do not employ phenotypic matching, offspring may simply be born with a randomly acquired signature. That is, a developing infant has the neural and anatomical capacity to produce an individualized signal within the acoustic range of the species. The distinctiveness of the signal is likely determined at some critical point in the development of the animal (Beecher 1982). In South American fur seals, there appeared to be no relationship between the call structure of pups born to the same mother in different years (Figure 7-2), although sample sizes were very low. Similarly, calls of twin big brown bat (*Eptesicus fuscus*) pups were also no more similar than the calls of unrelated pups (Rasmuson and Barclay 1992). These results further support the suggestion that in some species, individual signatures are most likely acquired at random.

Re-sighting of tagged animals and the use of DNA microsatellite markers have shown that both male and female South American fur seals exhibit fidelity to the area of the breeding beach in which they were born (Gemmell 1996; P. Majluf, unpubl. data). If individual vocal signatures of pups resembled those of their parents (whether by inheritance or by mimicry), then eventually particular areas of the beach would consist of animals with similar signatures. In terms of mother-pup recognition, this might be maladaptive because signature information would become more difficult to interpret, possibly to the point of being eliminated (Scherrer and Wilkinson 1993). Although female fur seals must spend time learning the signature calls of their pups, the random acquisition of individual signatures in fur seal pups is likely beneficial for maximizing recognition on crowded breeding beaches.

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Table 7-1. Results of one-way ANOVA (F-ratios) within mother-pup pairs, on each acoustic structure. df = 1,36. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

	Mother-pup pair									
	N408		N410		N418		N434		XX26	
Variable	F	p	F	p	F	p	F	p	F	p
DUR	24.8	***	37.7	***	55.9	***	92.1	***	77.20	***
NPARTS	191.8	***	12.5	**	0.6	ns	4.4	*	9.1	**
HI	–	–	9.2	**	18.7	***	59.5	ns	128.0	***
INF	64.8	***	29.8	***	47.9	***	66.2	***	216.7	***
MAXF	60.1	***	8.7	**	12.5	***	74.9	***	209.9	***
ENDF	150.9	***	14.8	***	37.7	***	44.5	***	169.9	***
PEAK1	29.7	***	18.4	***	55.6	***	141.8	***	357.9	***
PEAK2	3.9	ns	73.0	***	46.0	***	71.5	***	333.2	***
PEAK3	0.1	ns	179.8	***	47.4	***	46.9	***	191.5	***
AMP2	13.8	***	0.03	ns	13.5	***	16.3	***	12.2	**
AMP3	49.8	***	0.6	ns	29.1	***	95.3	***	7.0	*
FMP	3.1	ns	3.3	ns	29.6	***	21.1	***	–	–
FMR	2.4	ns	3.0	ns	14.9	***	6.4	*	–	–

	XX54		XX70		XX77		XX80		XX98	
Variable	F	p	F	p	F	p	F	p	F	p
DUR	53.8	***	23.4	***	21.5	***	115.6	***	45.4	***
NPARTS	1.5	ns	145.6	***	20.7	***	28.2	***	3.7	ns
HI	0.5	ns	–	–	90.8	***	–	–	86.4	***
INF	127.1	***	566.9	***	126.8	***	113.0	***	63.9	***
MAXF	21.1	***	1895.5	***	247.0	***	198.2	***	49.4	***
ENDF	40.8	***	424.0	***	109.4	***	137.1	***	29.7	***
PEAK1	60.8	***	2730.2	***	341.0	***	211.1	***	160.3	***
PEAK2	106.9	***	468.9	***	149.4	***	50.1	***	125.9	***
PEAK3	57.4	***	596.3	***	328.1	***	45.7	***	79.3	***
AMP2	2.4	ns	17.2	***	28.4	***	5.2	*	14.1	***
AMP3	0.3	ns	3.1	ns	12.6	**	37.7	***	30.5	***
FMP	5.1	*	12.9	***	201.9	***	11.0	**	23.0	***
FMR	5.7	*	17.7	***	168.8	***	12.2	**	35.0	***

Table 7-2. **Regression statistics comparing acoustic structures of calls of mother and pup South American fur seals, arranged in descending order of significance.**

Variable	n	r^2	b	S.E. (b)	F [a]	p
DUR	10	0.67	0.63	0.16	16.14	0.004
PEAK1	10	0.42	-0.67	0.28	5.73	0.04
MAXF	10	0.41	-1.26	0.53	5.63	0.05
HI	7	0.43	-1.49	0.78	3.71	0.12
AMP2	10	0.11	0.18	0.18	1.00	0.35
ENDF	10	0.10	-0.54	0.59	0.85	0.38
PEAK3	10	0.04	-0.28	0.50	0.31	0.59
PEAK2	10	0.03	-0.15	0.28	0.27	0.62
NPARTS	10	0.03	-0.44	0.88	0.25	0.63
INF	10	0.03	-0.24	0.50	0.23	0.64
AMP3	10	0.02	0.13	0.39	0.13	0.73

[a] df = 1,8

Table 7-3. Classification of calls of South American fur seal pups to their mothers, based on the discriminant function analysis. The number of calls assigned correctly is indicated in bold type.

			Mother to which calls were assigned									
Pup	n	%	N410	N408	N418	N434	XX26	XX54	XX70	XX77	XX80	XX98
N410	17	12	**2**	1	2	-	-	1	-	11	-	-
N408	19	0	-	**0**	-	-	-	-	-	19	-	-
N418	20	0	-	10	**0**	-	-	5	-	5	-	-
N434	19	0	-	10	-	**0**	-	3	-	6	-	-
XX26	19	0	-	3	-	-	**0**	-	-	16	-	-
XX54	20	0	-	8	-	-	-	**0**	-	12	-	-
XX70	20	0	-	1	-	-	-	-	**0**	19	-	-
XX77	19	100	-	-	-	-	-	-	-	**19**	-	-
XX80	20	0	-	1	-	-	-	-	-	19	**0**	-
XX98	18	0	-	10	-	-	-	-	-	8	-	**0**
N	191											

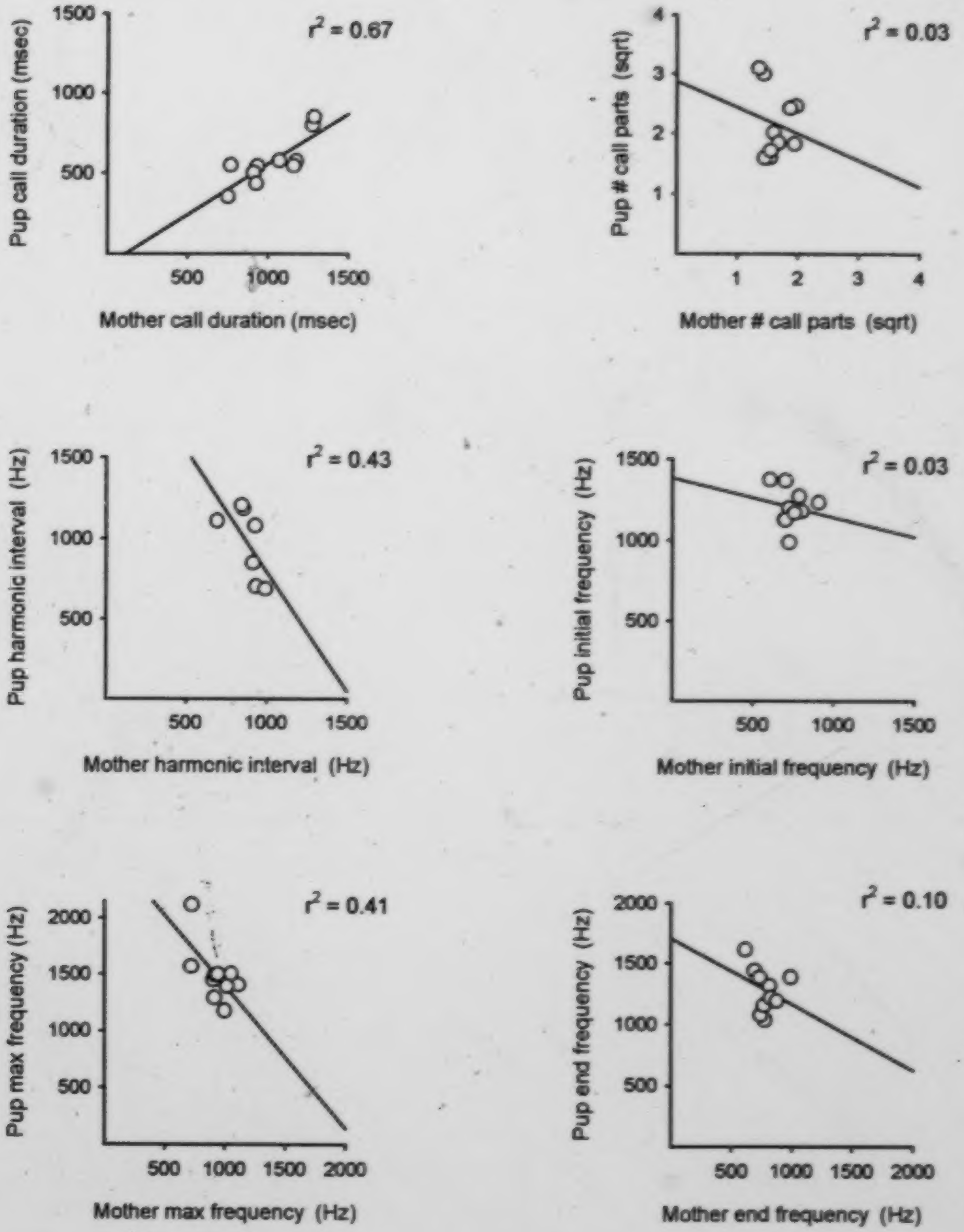

Figure 7-1a. Relationship of call characteristics between South American fur seal mothers and their pups. Points represent means for each pair. (Figure 7-1 cont'd on next page)

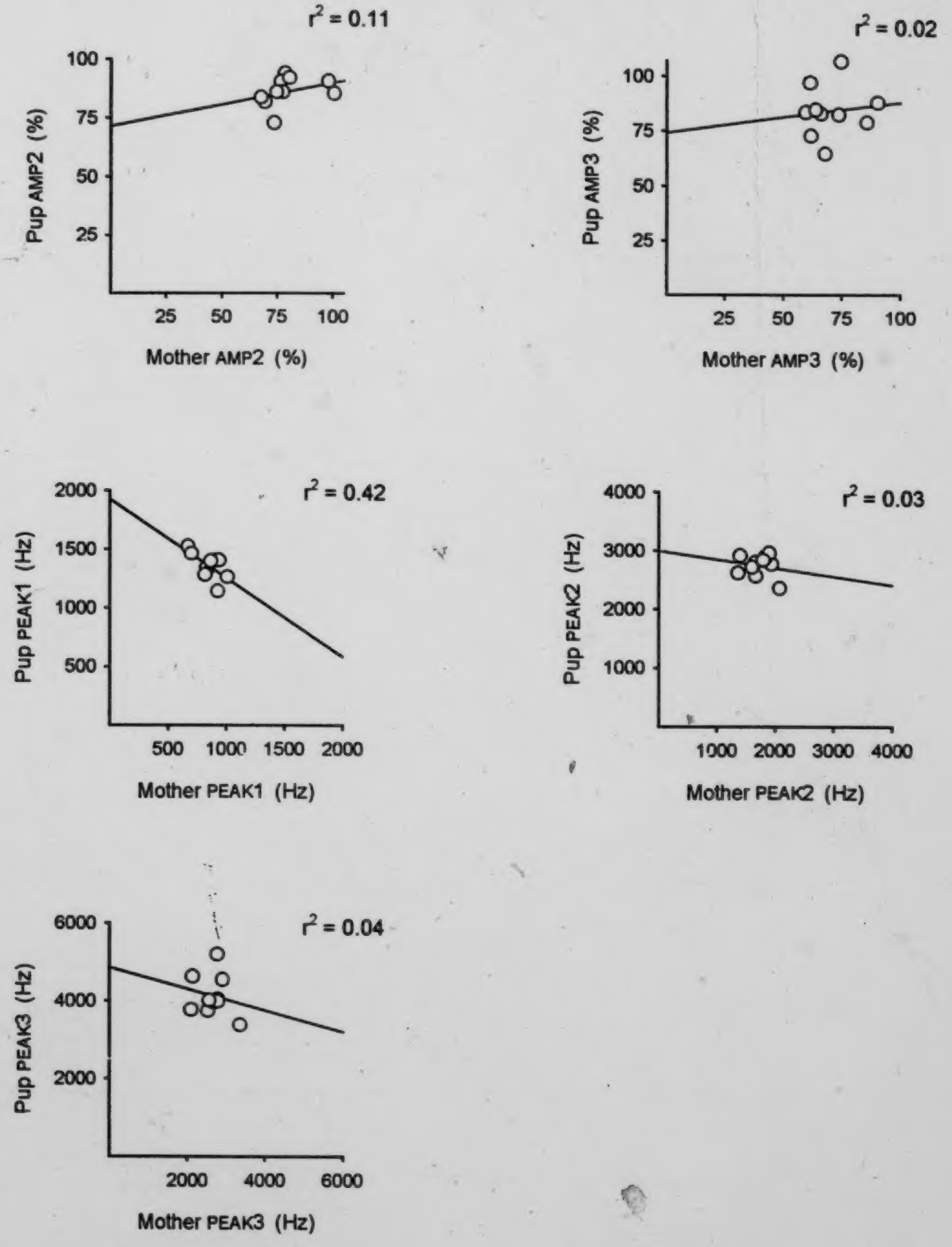

Figure 7-1b. Relationship of call characteristics between South American fur seal mothers and their pups. Points represent means for each pair. (Cont'd from previous page)

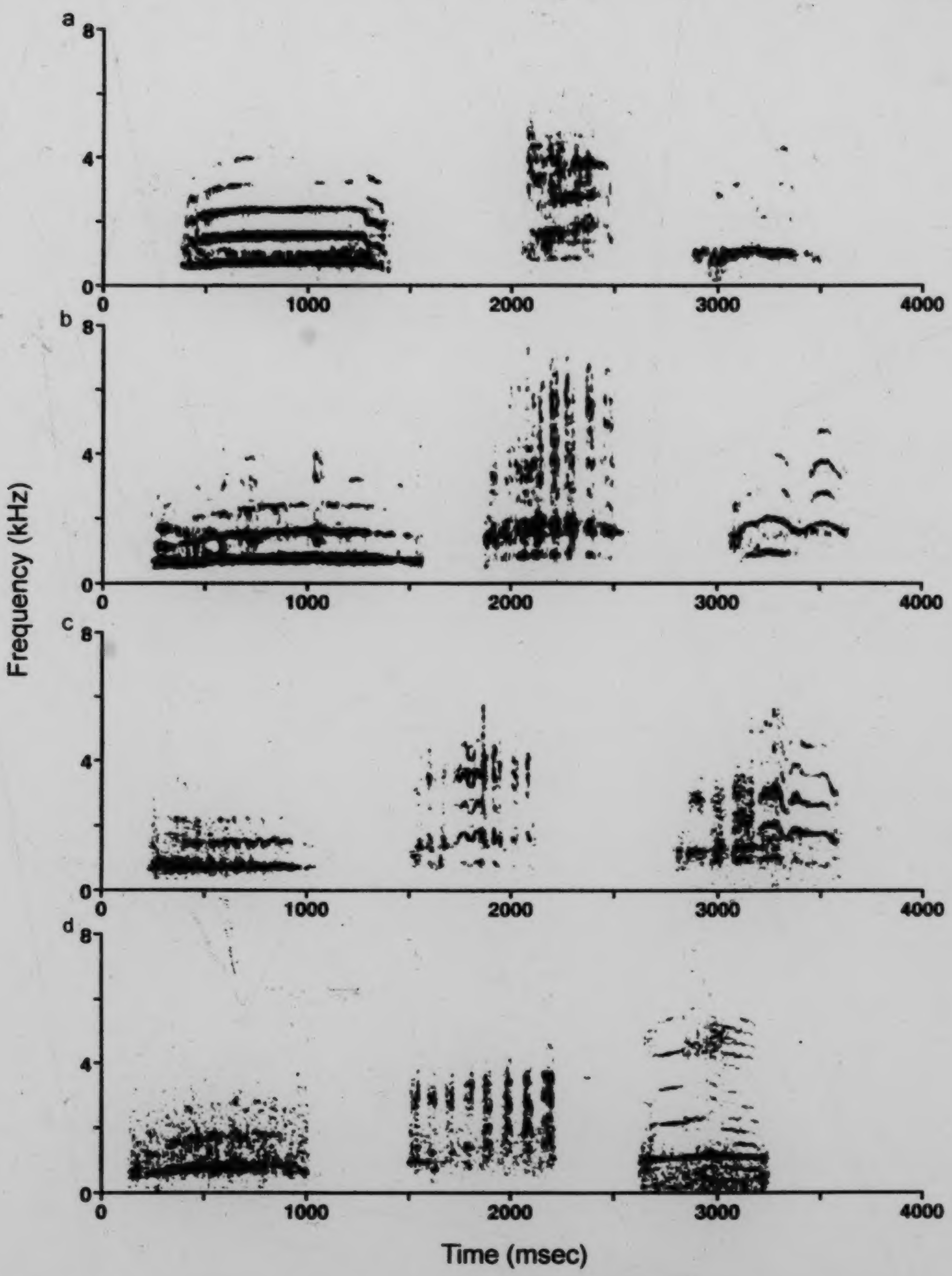

Figure 7-2. Representative spectrograms of calls of four different South American fur seal mothers (left) and their pups from 1994 (middle) and 1995 (right). Frequency bandwidth of spectrograms = 39 Hz.

8.0 CONCLUSIONS AND RECOMMENDATIONS

8.1 Summary

In this thesis I have investigated aspects of vocal communication and mother-pup behaviour of South American fur seals (*Arctocephalus australis*) breeding at Punta San Juan, Peru. As with most pinnipeds that breed in colonies, this population of fur seals experiences a number of factors which make consistent maternal care difficult (reviewed in Gentry and Kooyman 1986). In particular, the lactation period of up to 12 months requires mothers to frequently leave their pups unprotected in the colony while they forage at sea for days at a time, and mothers must reunite with their pups quickly upon return to ensure that pups are nourished and that maternal effort is not misdirected. At Punta San Juan, other factors also influence the ability of adult female South American fur seals to successfully rear offspring. These include overcrowding due to long-term disturbance and hunting pressure by humans that has resulted in limited protected habitat suitable for breeding, predation on pups by South American sea lions (*Otaria byronia*), and intense thermoregulatory effects that cause females to make daily movements through the colony. The combination of these factors has resulted in high levels of maternal aggression and subsequent pup mortality due directly to injury from unrelated adult females and indirectly to disturbances on the beach leading to separation of mothers from pups (Harcourt 1991, 1992; Majluf 1987; 1992). I hypothesized, therefore, that communication would be important to South American fur seals at Punta San Juan, for minimizing physical aggression and maintaining contact between mothers and pups throughout the lactation period.

To investigate the range of sounds produced by South American fur seals, I first attempted to describe the vocal repertoire of the species (Chapter 3). Note that my study was limited to vocalizations produced in air during the breeding season; caution should be used in extrapolating these results to underwater sounds or to communication outside of the context of breeding and rearing offspring. Both male and female South American fur seals at Punta San Juan produce a large range of vocalizations. Most of these are similar to those described for other species of the genus *Arctocephalus*. In particular, barking, threat calls used by adult males and calls used between mothers and pups have been frequently reported in the literature. In this study, however, I found that adult females used most of the threat calls previously attributed only to adult males, albeit less frequently. The threat calls of South American fur seals appear to show gradation of structure, form and apparent meaning. I suggest that this might be adaptive for enabling flexible display behaviour in agonistic situations, allowing participants to interpret the situation based on contextual cues and their own physical ability and previous experience. In contrast, vocal displays such as submissive calls, full threat calls and affiliative calls used between mothers and pups tended to have a discrete acoustic structure, although variation of the basic form of the calls appeared to allow for individuality of vocal signals.

The level of aggression exhibited by adult female South American fur seals is driven primarily by a combination of high breeding densities and the animals' need to make daily thermoregulatory movements in response to thermal stress. In Chapter 4, I explored some of the social, environmental and ecological factors which might further influence aggressive behaviour by females. Agonistic calling by females (to both males and females) appeared to increase as a function of climatic conditions such as warm temperatures and low cloud cover, as did the rate of barking by males to females, probably due to the number of disturbances occurring in males' territories. However, these factors seemed to have little effect on the rate at which mothers called to their pups, which remained relatively high throughout the day. On beach N4, where most of my research was conducted, frequent intrusions by South American sea lions resulted in disturbances of the fur seal colony, ranging from localized vigilance to complete stampedes. I suggest that the combination of these factors, which may not occur in other populations of South American fur seals or other species of otariids, may contribute to the disproportionately high levels of female aggression at Punta San Juan recorded by Harcourt (1991, 1992) and Majluf (1989, 1992). These preliminary observations may indicate some areas for future investigation.

High levels of maternal aggression are likely to increase the cost of maternal care for South American fur seals, because disturbances among females make locating and maintaining contact with pups more difficult. Therefore, both mother and pup South

American fur seals were expected to exhibit behavioural adaptations which might facilitate reunion (Chapter 5). Mothers use geographic and spatial cues to orient to the natal beach, and consistently return to an apparently preferred region of the beach that I referred to as the "home spot". At beach N4, going to the home spot did not make searches more successful, but this colony was small both in area and population. In larger breeding beaches, mothers' tendencies to visit their home spot might be adaptive because it would reduce the size of the area in which mothers and pups might expect to find one another. Pups appeared to play an important and active role in the reunion process, as only pups that vocally responded and/or moved towards their mothers were reunited. The differential response by pups to their mothers, compared to unrelated females, suggests that pups can probably discriminate their mothers' calls from a distance, which is adaptive in this population to avoid injury from other females.

As in other otariids, vocal cues appeared to be the most important for recognition between mothers and pups, particularly over long distances. An acoustic analysis showed that both pup-attraction calls and female-attraction calls exhibit sufficient call stereotypy (i.e. low variability within and high variability among individuals) that individuality of calls is likely (Chapter 6). The statistical procedures I used in this study were able to discriminate among individuals based on linear combinations of various acoustic characteristics. In particular, characteristics of the fundamental frequency appeared to be most important for distinguishing among adult females, while pup calls, which typically contained less harmonic structure, could be differentiated by formant-like frequency ranges. Although this analysis has shown that mother and pup calls are individualistic, there is still no evidence that South American fur seals are sensitive to or make use of the acoustic characteristics I measured in order to recognize individuals. However, observations of searching and reunion behaviour (Chapter 5) do suggest that these vocalizations are important cues to recognition between mothers and pups.

For mothers and pups to recognize one another, the acoustic structure of pup calls might be inherited or learned from the mother, allowing phenotypic matching to occur. In the absence of acoustic similarity between mother and pup calls, both individuals would need to learn each other's call to enable recognition. Thus, I compared the acoustic characteristics of calls of mothers and pups, including pups born to the same mother in two seasons (half-siblings) (Chapter 7). Based on the acoustic variables I used, I found no consistent trends between calls of related individuals, suggesting that learning of each others' calls is required. This likely occurs during the perinatal attendance period, although if pups' calls change during development, mothers would have to continuously update their memory. That pups appear to have acoustically different calls from those of their mothers and siblings is likely adaptive for the population of fur seals at Punta San Juan, because natal site fidelity appears to result in groups of related individuals in similar areas of each breeding colony. Thus, random acquisition of pup calls might maintain the diversity of vocal signatures within the colony.

8.2 Recommendations for future research

The findings of this study demonstrate the use of vocal communication to South American fur seals at Punta San Juan, Peru, particularly by mothers and pups. Numerous aspects of vocal communication in this species remain to be investigated, including the form and function of vocalizations used underwater; the possibility of individuality of full threat calls, especially among territorial males; and the relationship between submissive and juvenile calls and the motivational or affective state of the sender (Scherer 1985), to name but a few. However, in this section I limit suggestions for future research to two of the main themes of this thesis: vocal development in pups, and the use of aggressive vocalizations, particularly by females.

8.2.1 Ontogeny of otariid vocalizations

In this study, I was limited to pups less than six weeks old; thus, I could only speculate on possible effects of ontogeny over that time (see Chapter 6 and Appendix C). However, given the acoustic complexity of female-attraction calls and the observations that pups also produce growls and puffs at an early age (Chapter 3), it is likely that fur seal pups are capable of producing the basic vocal elements required for the range of calls used by adults. To better understand vocal behaviour of otariids, there is a need for longitudinal studies of individuals, to document the anatomical and acoustical changes related to vocalization as the animals mature. Specifically, virtually nothing is known of the structure and range of calls used by fur seals from about 6 months of age to the time they are reproductively active (approximately 4 years of age for females; 9 - 14 years for males).

Some studies have noted structural similarities between calls used by fur seals in different stages of development (Bartholomew and Collias 1962; Shipley *et al.* 1986; E.H. Miller, unpubl. ms.). In this study I also noted that the full threat calls, pup-attraction calls and female-attraction calls produced by South American fur seals also share some features (both structural and functional) in common (Chapter 3), although individuality of calls made by mothers and pups appeared to be based on different acoustic characteristics (Chapter 6). Might the affiliative calls used by pups be a developmental precursor to the "adult" pup-attraction calls and full threat calls? A structural comparison of these acoustically complex calls might provide more information on the way calls develop with age. Sex-related differences in ontogeny are also required, because in this study adult female South American fur seals produced both pup-attraction calls and full threat calls. If females of other species are also found to produce full threat calls (see below), a structural comparison of these two types of calls would be informative.

8.2.2 Aggressive vocalizations and the problem of inconsistency in the literature

Adult female South American fur seals are more aggressive to conspecifics than any other species of fur seal studied to date (Harcourt 1991, 1992; Majluf 1987; 1992). This was reflected in the range and frequency of agonistic calls used by adult females in this study. Note that in this study, investigations of agonistic interactions were limited to vocal behaviour. Other studies have shown that visual displays such as open-mouth threats are used more frequently than vocalizations (e.g. Carey 1992), so caution should be used when comparing my estimates of agonistic behaviour with others reported in the literature. Nonetheless, two conclusions could be made about the usage of threat calls by adult female South American fur seals at Punta San Juan compared to females of other populations and species. The first is that all female fur seals might have the vocal ability to produce the range of graded respiratory and guttural threat vocalizations that I observed in this study, even though they are rarely used in most species. As suggested in Chapter 4, fur seals at Punta San Juan might be subjected to a unique combination of factors not experienced by other species. The high level of aggression among adult female South American fur seals might therefore have resulted in selective pressures on females to use more of the range of vocal threat signals than is used by females of other species. Alternatively, the usage of threat calls by females might have been under-represented in the literature. In many studies, threat calls have been named "male" calls, so there may have been a bias towards males when describing such calls. Also, most studies of female behaviour in otariids have focused on reproductive behaviour or mother-pup interactions, while those few studies which included female aggression have tended not to incorporate vocal components. It is therefore possible that vocal threat behaviour among females might simply have been overlooked or confused with other calls if they were used infrequently. Regardless, the absence of information about female aggressive vocalizations in the literature is more likely a reflection of the difficulty associated with describing and quantifying behaviours that are subtle or occur rarely (Lehner 1979), rather than their absence.

Studies of vocal behaviour in *Arctocephalus* and other otariids have produced a multitude of terms for guttural and respiratory threat calls (Table 3-1), which have led to some confusion in the literature. For example, Pierson (1987: 87) describes a "boundary puff" as "a single sharp exhalation of air, which results in a harsh, puffing sound" and reports that it corresponds to the "male gutteral challenge" (*sic*) of Stirling and Warneke (1971). However, after examination of Pierson's spectrogram (his Fig. 5b) and his description of the behavioural context of the call, I believe that the call corresponds best to what I have termed a chuff. This example illustrates the difficulty of using onomatopoetic descriptions to name and analyze graded sounds (Marler 1976; Green and Marler 1979; Morton 1982; Miller 1991).

I believe that there is a need for standardization of nomenclature and acoustic analysis in research on pinniped vocal behaviour, as suggested by Stirling and Roux (1987) and Miller (1991). The availability of quantitative information on acoustic structure and call usage would enable interspecific comparisons of behaviour which can address evolutionary and ecological questions about the phylogeny of the various pinniped taxa (e.g. Repenning *et al.* 1971; Berta and Wyss 1994; Lento *et al.* 1997).

My study is one of few that has attempted to quantify call usage in otariids. This was important, because by verifying which calls were being used in which contexts, I reduced the bias inherent in some of the call names (eg. female-attraction call). As shown in Table 3-1, previous studies have employed call nomenclature based on either the acoustic features of the call or its presumed function. Names which are based on functional or interpretive descriptions, such as "female-attraction" or "full-threat" run the risk of being used inappropriately, or used in an over-generalized way (Lehner 1979; Miller 1991; Miller and Job 1992). Conversely, in order to compare across populations or species, purely empirical names such as "mother primary call" (Insley 1989, 1992) must be accompanied by a description of either the acoustic characteristics or the context in which the call is most often used. Many studies, including this one, have also borrowed terms from common usage in the English language (e.g. roar, growl, belch, whimper, bark). Although these do not directly describe a function, there is a risk that some readers might associate their context with those of mammals they are more familiar with such as bears, dogs and cats.

Regardless of the system of nomenclature used, it is important in studies such as these to clearly define the terms used for specific vocalizations and behaviours, and not to adopt terms from the literature without confirming that they are applicable to the species and circumstances under study. Careful examination of the literature is also required to ensure that a single behaviour does not receive a multitude of names and ascribed functions. Also, there is a need to quantify the response of the receiver, to better understand the potential meanings of the calls, particularly those used in agonistic situations. As Paton (1987: 171) noted, "if the recipient - the individual to whom the signal is of most relevance - fails to make a distinction between [signals], we have no evidence that the behaviour patterns constitute different signals, no matter how different their respective forms may be."

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APPENDIX A: Supplementary data and list of tagged fur seals used in this study

Table A-1. Individual fur seals tagged at N4 for use in this study.

Year	Mother tag #	Pup tag #	Sex of pup	Comments
1994	XX40	XX41	M	Retagged in 1995 (N438)
	XX44	XX45	M	
	XX52	XX47	F	
	XX54	XX71	M	
	XX57	XX56	F	Retagged in 1995 (N414)
	XX58	XX59	F	
	XX60	–	F	Pup died 941111
	XX64	XX67	M	Retagged in 1995 (N432)
	XX68	XX63	M	
	XX70	XX69	F	
	XX74	XX75	F	
	XX77	XX73	F	Pup died 941128
	XX80	XX27	F	Pup present as yearling in 1995
	XX88	XX87	F	Pup died 941126
	XX93	XX95	M	
	XX98	XX99	F	
	–	XX26	F	
	–	XX51	M	
		"C1"	?	See below *
1995	N402	N401	F	
	N404	N403	F	
	N406	N405	F	
	N408	N407	M	
	N410	N409	F	
	N412	N411	M	
	N414	N413	M	Pup died 951213
	N416	N415	M	
	N418	N417	M	
	N420	N419	M	Pup died 951124
	N422	N421	F	
	N424	N423	F	
	N426	N425	F	
	N428	N427	M	
	N430	N429	M	Pup died 951207
	N432	N431	F	
	N434	N433	F	
	N436	N435	M	
	N438	N437	F	
	N440	N439	F	
	N442	N441	F	
	N444	N443	F	Pup died 951204
	N446	N445	M	
	–	N447	F	Pup died 951210
	–	N448	M	
	–	N449	M	
	–	N450	F	

* This pup was the first pup born on beach N4 in 1994 season (Oct 20). As it was the only pup on the beach, I was able to reliably identify it for 11 days until the second pup was born on 31 Oct. Called "C1" on tape.

Table A-2. Other tagged fur seals used in this study. These animals were tagged prior to 1994, on Beaches N4, N5 or S3.

Mother tag #	Pup tag #	Sex of pup	Year tagged
090	–	F	1990
455	–	F	1986
H49	–	M	1988
L81	–	F	1989
S62	–	M	1992
S66	–	M	1992
X32	–	M	1993
X72	–	?	1993

Table A-3. Distribution (%) of calls made by adult male fur seals prior to and during the onset of the 1995 pupping period. (n = number of sampling periods; N = number of calls observed in each category, pooled across all sampling periods). Values of .0 indicate proportions < 0.05%.

a) No pups (n = 52)

	Recipient of call						
Call type	Female	Male	Pup	Juv.	Colony	Unclass.	N
Barking	44.4	3.1	–	1.6	1.9	4.1	502
Threat calls (total)	5.1	34.8	–	.9	1.9	1.3	401
Puffing	.2	9.6	–	.2	–	–	92
Chuff	–	0.1	–	–	–	–	1
Growl	4.7	9.0	–	.7	.4	.6	140
LITC	.1	7.3	–	–	.4	.4	76
Guttural threat call	–	1.6	–	–	.3	.1	19
Full threat call	–	7.1	–	–	.7	.2	73
Submissive calls	–	.2	–	–	–	–	2
Affiliative calls	–	–	–	–	–	–	0
Unclassified	–	.7	–	–	–	.2	8
N	451	354	0	23	34	51	913

b) Onset of pupping (n = 33)

	Recipient of call						
Call type	Female	Male	Pup	Juv.	Colony	Unclass.	N
Barking	47.3	4.5	.8	.7	.7	2.3	486
Threat calls (total)	2.7	39.0	–	.3	.3	.2	367
Puffing	.8	8.5	–	.1	–	–	81
Chuff	–	2.1	–	–	–	–	18
Growl	1.9	9.1	–	.2	.1	.1	98
LITC	–	1.9	–	–	–	.1	17
Guttural threat call	–	.7	–	–	–	–	6
Full threat call	–	16.8	–	–	.2	–	147
Submissive calls	–	–	–	–	–	–	0
Affiliative calls	–	–	–	–	–	–	0
Unclassified	.2	.8	–	–	–	–	9
N	433	382	7	9	9	22	862

Table A-4 Distribution (%) of calls made by adult female fur seals prior to and during the onset of the 1995 pupping period. (n = number of sampling periods; N = number of calls observed in each category, pooled across all sampling periods). Values of .0 indicate proportions < 0.05%.

a) No pups (n = 52)

	Recipient of call						
Call type	Female	Male	Pup	Juv.	Colony	Unclass.	N
Barking	.1	–	–	.0	–	.0	7
Threat calls (total)	57.1	14.3	–	8.6	.0	4.0	5117
Puffing	10.6	.9	–	.7	.0	.3	761
Chuff	–	–	–	–	–	–	0
Growl	46.3	13.4	–	7.8	.0	3.7	4338
LITC	–	.0	–	.0	–	–	3
Guttural threat call	.2	.0	–	.0	–	–	15
Full threat call	–	–	–	–	–	–	0
Submissive calls	7.1	.5	–	–	–	.1	461
Affiliative calls	–	–	–	7.3	.0	.4	473
Unclassified	.2	.0	–	–	.0	.3	34
N	3924	902	0	968	5	293	6092

b) Onset of pupping (n = 33)

	Recipient of call						
Call type	Female	Male	Pup	Juv.	Colony	Unclass.	N
Barking	.5	–	–	.0	–	–	19
Threat calls (total)	37.9	10.8	.3	4.0	.1	1.3	1848
Puffing	13.4	.8	.1	.6	–	.4	522
Chuff	–	–	–	–	–	–	0
Growl	24.4	10.0	.2	3.4	.1	.8	1319
LITC	–	–	–	–	–	–	0
Guttural threat call	.2	–	–	–	–	.0	7
Full threat call	–	–	–	–	–	–	0
Submissive calls	6.2	.2	–	–	–	–	219
Affiliative calls	–	.0	31.1	5.2	.3	1.8	1308
Unclassified	.2	.0	.1	–	–	.1	11
N	1526	377	1071	312	12	107	3405

APPENDIX B: Glossary of acoustic terms used in this study

The following glossary summarizes information from several key publications on acoustic analysis (Watkins 1967; Marler 1969; Fry 1979; Green and Marler 1979; Beecher 1988; Lieberman and Blumstein 1988; Robinson *et al.* 1988; Denes and Pinson 1993; Owren and Linker 1995; Todt *et al.* 1995).

Sound production

Glottal source - the larynx, an anatomical structure composed of the glottis and vibrating vocal folds, which produces the fundamental frequency of sound in mammals.

Supraglottal sources (a.k.a. supralaryngeal sources) - the tissues and cavities found above the larynx (including the pharynx, oral cavity, nasal cavity), which strongly influence the glottal waveform through their resonance (amplification) and anti-resonance (damping) qualities.

Resonance (formants) - the alteration (both by damping and amplification) by the supraglottal structures of the signal produced by the glottal source. Since the supraglottal structures move independently of the vocal folds, formant frequencies are independent of the harmonic frequencies of the sound.

Tonality

Tonal sounds - have a fundamental frequency and/or corresponding harmonics, and are produced by periodic vibration of the vocal folds. Tones are characterized by a regularly repeating waveform.

Fundamental frequency (F_0) - the rate of vibration of the vocal folds.

Harmonics - frequency bands that are integer multiples of the fundamental frequency (a.k.a. the first harmonic). The frequency of the second harmonic is twice that of F_0, the third harmonic is three times the F_0, and so on. Thus, the **harmonic interval** is the same as the fundamental frequency.

Resonant frequencies (formants) - frequency bands caused by supraglottal modification of the sound produced by the vocal folds.

Pulsing

Non-tonal sounds (a.k.a. atonal, aperiodic sounds) - sounds that have no harmonic basis. These sounds are typically perceived by the human ear as noise rather than tone.

Pulses - brief, non-tonal sounds caused by constriction of the vocal tract at some point. As air passes through the constriction, it becomes turbulent and moves at random, causing components (of more or less equal amplitude) at all frequencies, rather than only at multiples of a fundamental frequency. These sounds will produce a spectrogram that exhibits many frequency bands, which have often been erroneously described as harmonics (see Watkins 1967).

Guttural sounds - when pulses are produced at a low enough rate (frequency), the sound is heard as a series of distinct pulses rather than a single, noisy sound.

Acoustic analysis

Sampling rate - rate at which signal is acquired during digitizing, which must be at least twice that of the Nyquist frequency (maximum frequency) of the signal. If the sampling rate is lower than this, higher-frequency components of the sound are inaccurately represented on spectrograms as energy occurring at lower frequencies.

Fast Fourier Transform (FFT) - a mathematical algorithm used to transform data from the time domain to the frequency domain, producing a **spectrum**, or distribution of amplitude across frequencies in a specified interval of time. The FFT is frequently used to compute series of spectra to form a spectrogram.

Power spectrum - a discrete Fourier transform (DFT); frequency spectrum representation based on a short-time analysis window.

Intensity - a measure of the energy transmitted along the sound wave, per cm^2. Decibels (dB) are a measure of the relative intensity of the sound compared to a standard intensity (10^{-16} watts / cm^2)

Loudness - the subjective correlate of intensity as perceived by the receiver of the sound. The judgement of loudness may be affected by other factors (such as frequency, duration).

Pitch - the subjective correlate of frequency as perceived by the receiver of the sound. When a complex sound consists of several frequencies differing by a constant amount (e.g. harmonics), the perceived pitch is often that of a tone whose frequency is equal to the common difference.

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APPENDIX C: Early ontogenetic effects on pup call structure

The young of many colonially breeding species of birds and mammals are precocious, and begin vocalizing soon after hatching or birth. Typically, the offspring's call facilitates recognition by its parent(s) amidst the crowded colony. Several studies have shown that calls of very young colonial animals are relatively unstructured at first, and that the call stabilizes over time (e.g. bank swallows, *Riparia riparia* (Beecher *et al.* 1981); vervet monkeys, *Cercopithecus aethiops* (Seyfarth and Cheney 1986); lesser spear-nosed bats, *Phyllostomous discolor* (Esser and Schmidt 1989)). Similarly, otariid pups are known to start vocalizing soon after birth, and Peterson and Bartholomew (1969) and Stirling (1971) have suggested that female-attraction calls (FACs) appear to become less variable with age. Therefore, I investigated the hypothesis that ontogeny affects the variability of a pup's call to determine whether this might present a bias in the analysis of individual variation in pups.

I chose seven pups of known or reliably estimated ages for which I had recordings from two or more non-consecutive days. For some pups, recording sessions contained very few calls on a particular day; however, I included these days even though the resulting sample sizes ranged from 4 to 20 calls. Acoustic variables were measured as described in Appendix E, except that the variable NPARTS was not used in this analysis. For each variable within each pup, I used one-way Kruskal-Wallis tests to examine absolute differences in call structure among days. Coefficients of variation (CV = standard deviation / mean) were calculated for each combination of acoustic structure, day and pup, and subjected to Friedman's tests (pups with more than two days' recordings) or Wilcoxon signed-ranks tests (pups with two days' recordings), in which days and acoustic variables were considered to be treatments and blocks, respectively (Sokal and Rohlf 1981).

Overall, the age of the pup did not significantly affect the variability of its calls (Figure C-1, Table C-1). However, plots of CV as a function of age revealed a trend for certain variables (Figure C-2). Also, calls from the youngest pup, C1, were the most variable (Figure C-1) and this approached significance ($p = 0.054$). Values of CV appeared to be variable up to eight to ten days, but remained about the same thereafter. This does not imply that the pups' calls are stereotypical among individuals by this age, but merely that the variation within the calls of an individual appears to stabilize by about eight days.

Otariid mothers and pups are known to vocalize most frequently during the perinatal period (e.g. Peterson and Bartholomew 1969; Trillmich 1981). The results of this analysis suggest that the structure of pups' calls appears to stabilize around eight to ten days, coinciding with the age at which mothers typically leave for their first foraging trip. Therefore, there might be selective pressures acting on pups to fine tune their calls before their mothers depart. This would facilitate recognition of pups by their mothers when they return to the breeding colony. Therefore, I limited the selection of calls for the analysis of individuality (Chapter 6) to pups at least eight days old. Calls of pups above this age were assumed to have equivalent levels of variability.

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Table C-1. Variation in overall acoustic structure (based on mean coefficient of variation of all acoustic variables) for South American fur seal pups up to 21 days old.

Pup	Age (days)	n (# calls per day)	Test statistic [a]	df	p
C1 [b]	1,2,3,6,8	18,12,20,10,6	9.283	4	0.05
N433	3,8,10	19,13,12	1.273	2	0.53
XX99	3,12,17	17,6,11	2.167	2	0.34
N407	8,20	20,8	1.481	1	0.14
N437	7,10	20,4	1.007	1	0.31
XX27	13,21	19,16	0.357	1	0.72
XX71	8,11	9,13	0.255	1	0.80

[a] Friedman Test (chi-square) for first three pups; Wilcoxon signed-ranks test (Z) for rest.

[b] See Table A-1.

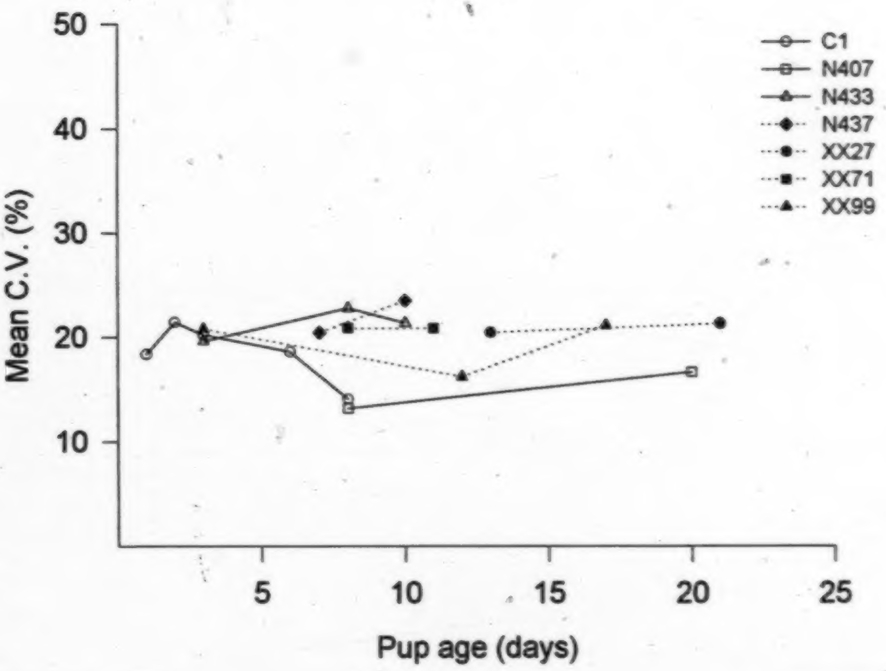

Figure C-1. Effect of pup on variability of call structure for seven South American fur seal pups. Values shown are C.V. (coefficients of variation) averaged over all acoustic structures.

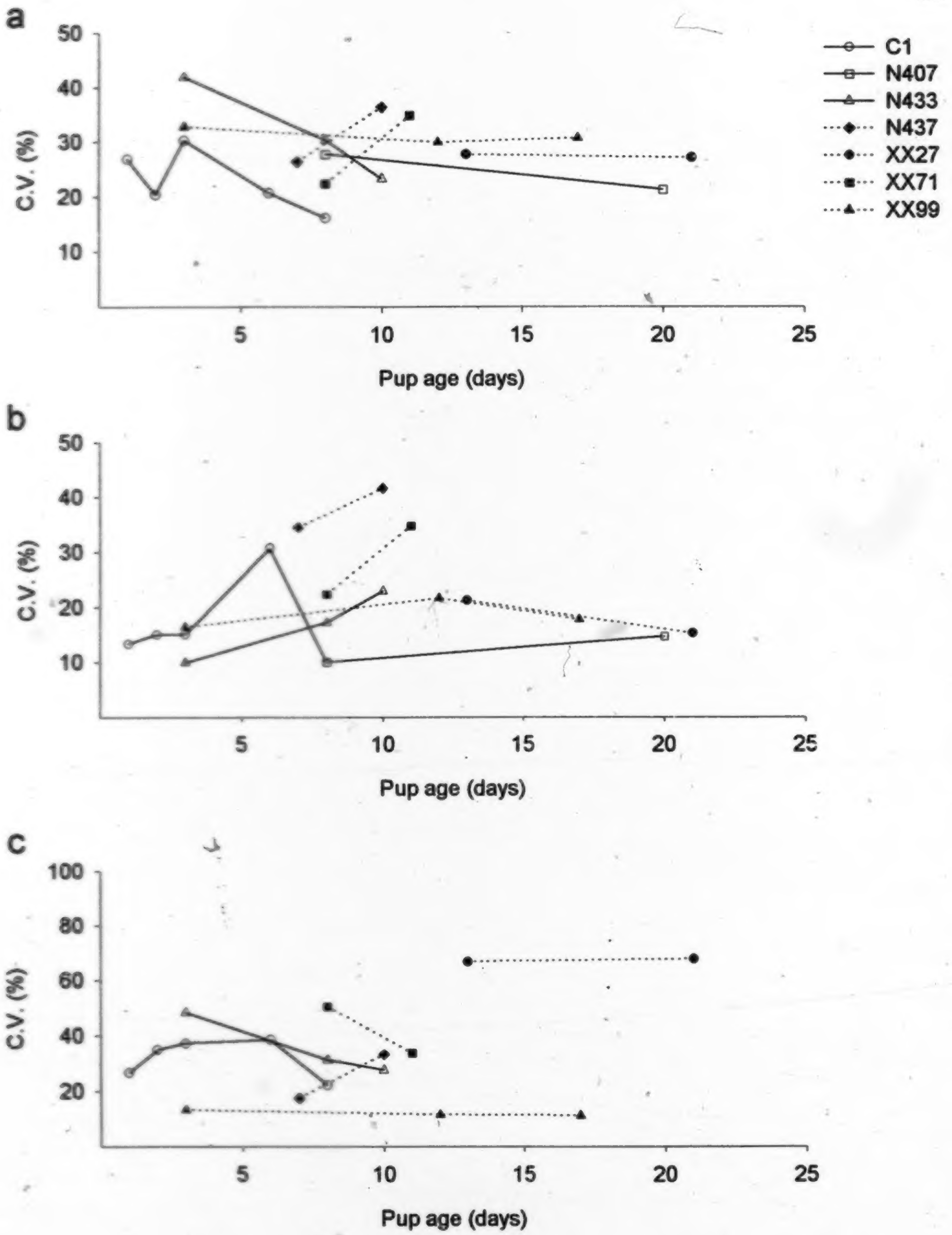

Figure C-2. Variation of a) call duration; b) end frequency; c) harmonic interval over time for seven South American fur seal pups. Note different scale in c).

APPENDIX D: Variability of female calls under different contexts

Morton (1977, 1982) has suggested that the physical structure of mammal and bird vocalizations is affected by the motivational state of the sender. Thus, within the constraints of the repertoire of the species, animals tend to use higher-frequency, more tonal sounds when affiliative, and harsh, relatively low-frequency sounds when hostile.

At Punta San Juan, tagging activities provided opportunities for clear, close-up recordings to be obtained. However, the presence of humans on the beach is clearly disturbing to South American fur seal mothers. I hypothesized that female pup-attraction calls might exhibit increased variability of call structure due to varying motivational and emotional states of females in three different contexts: female arriving from sea ("reunion"), female already ashore for at least a day ("on-beach") and female recorded during tagging operations ("tagging"; excluding females which had been tagged that day).

Calling bouts from the first two contexts were recorded from the cliff-top, whereas in the latter situation, females were recorded on the beach from a distance of 1 - 3 m, while other humans were also on the beach. I chose calling bouts from seven females that had been recorded in at least two of the contexts, on separate days. Sample sizes ranged from 6 to 20 calls per context per female. Kruskall-Wallis tests and CVs were calculated as in Appendix C. Variability profiles were plotted for each context. These profiles simply represent a visual display of CVs for each acoustic variable and are not meant to imply continuity between the variables. The contours of each profile may be visually compared to explore differences in the level of variation between the groups (Sokal and Braumann 1980; see also Insley 1992, Fig. 5). I used a Friedman's test to detect differences in CV among contexts (treatments), using acoustic structures as blocks.

There were no detectable differences in call structure between contexts (Friedman's chi-square = 0.46; df = 2; p = 0.79; Figure D-1). This suggests that call stereotypy is not influenced by emotional or motivational state. Therefore, to examine individual variation in mother fur seal calls, it was not necessary to limit the sample to calls from a particular context.

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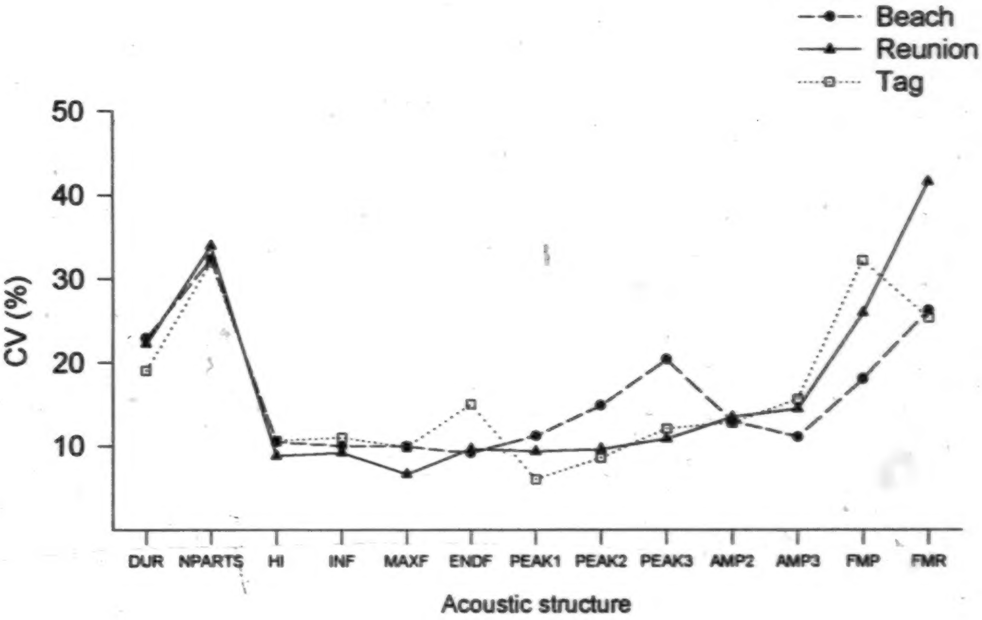

Figure D-1. Variability profiles of female call structures recorded in three contexts. Values are grand means of CV (coefficient of variation) over all females (n=7).

Appendix E: Measurement criteria for acoustic variables

Spectrographic analyses were conducted using the SIGNAL/RTS sound analysis package (Engineering Design, Belmont, Mass.). After a preliminary examination of spectrograms from females and pups, I determined sixteen variables which could be reliably measured for each call (Figure 6-1). Abbreviations are used as follows:

TONAL	Presence / absence of tonality (harmonic structure) within a call
PULSE	Presence / absence of pulsing within a call
FM	Presence / absence of rhythmic frequency modulation within a call
DUR	Duration of call (msec)
NPARTS	Number of parts per call
HI	Harmonic interval (Hz)
INF	Frequency of lowest harmonic at onset of call (Hz)
MAXF	Maximum frequency of lowest harmonic (Hz)
ENDF	Frequency of lowest harmonic at end of call (Hz)
PEAK1	Frequency of first energy peak (Hz)
PEAK2	Frequency of second energy peak (Hz)
PEAK3	Frequency of third energy peak (Hz)
AMP2	Ratio of amplitudes of the first and second energy peaks (%)
AMP3	Ratio of amplitudes of the first and third energy peaks (%)
FMP	Period of rhythmic FM, when present (msec)
FMR	Range of rhythmic FM, when present (Hz)

The categorical variables TONAL, PULSE and FM were coded as present (1) or absent (0). A call was considered to contain tonal regions if there was clear evidence of harmonic structure (regularly repeating horizontal bands) in at least one of the call parts (see below). Pulsing and FM were used as in Miller and Murray (1995). On narrow-band spectrograms, pulses were identified as regions appearing to consist of very closely spaced horizontal bands, or having no distinguishable structure (see also Watkins 1967). Pulses occurred on their own or overlaid other regions of a call. FM was defined as *rhythmic* frequency modulation of the harmonics of a call (contrasted with a non-cyclic change in the frequency of the harmonics). At least two cycles of FM had to be present in a call for it to be coded as present. By definition, calls with no tonal regions had no FM.

DUR was measured in the 39 Hz (narrow) bandwidth and cross-checked on the amplitude waveform display to control for smearing in the temporal direction, which is inherent in the narrow-band display. Other studies have typically employed a wide-band filter to measure temporal characteristics; however, wide bandwidths did not provide optimal resolution for these spectrograms. Beecher (1988) discusses this problem in more detail.

Parts (NPARTS) were defined as distinct regions which make up a call using two criteria: distinct amplitude modulation *and/or* a distinct change in the frequency characteristics of the call. Amplitude modulation was determined from the amplitude waveform. Parts were distinguished when the amplitude of a call decreased to "zero" (for this purpose, the level of ambient noise before and after the call) and then returned to the mean amplitude or higher. If the amplitude remained at zero for more than about 20 msec, a period of silence could be perceived between the call parts (Figure E-1a). Frequency characteristics were examined on spectrograms. Examples of distinct changes in the frequency characteristics of a call included a change from a pulsed region to a tonal region (Figure E-1b); sudden presence of FM within a tonal region (Figure E-1c) or sudden change in harmonic interval of the call, *sensu* Miller and Murray (1995) (Figure E-1d). If a tonal region was overlaid with pulses, the pulses were only counted as separate parts if the harmonic structure of the region was completely obscured (Figure E-1e). If the underlying harmonic structure could still be discerned through the pulses, the region was counted as one part (Figure E-1f).

HI, INF, MAXF and ENDF were measured from spectrograms. Since the fundamental frequency (or first harmonic) was not visible in many calls, the frequency variables were measured at the lowest visible harmonic (Figure E-2a,b). The harmonic interval, which is equivalent to the fundamental frequency, was measured as the distance (Hz) between the first two visible harmonics.

To characterize the FM in a call, the range and period of FM were measured. FMR is the amplitude of periodic (or cyclic) frequency modulation about the carrier frequency of the second (visible) harmonic, while FMP (strictly speaking, half the period) is the time between a consecutive peak and trough of a cyclic frequency modulation waveform, also measured on the second harmonic (Figure E-2c). I chose the second harmonic because cyclic frequency modulation was often not apparent in the first harmonic. If FMP or FMR varied substantially within a call, I calculated an average value.

Energy peaks (PEAK1, PEAK2 and PEAK3) were examined from power spectra, and refer to amplitude-emphasized frequency ranges (Figure E-3). In some cases, these energy peaks may represent the resonant frequencies of the vocal tract ("formants").

Within a call, amplitude may be affected by many factors, such as emotional state or fatigue in the vocalizing animal, movement (including head shaking) of the vocalizing animal, distance from and orientation to the microphone, background noise level and battery charge of the recording equipment. Therefore, estimates of amplitude were restricted to those of the energy peaks (AMP2 and AMP3), expressed as measurements relative to the amplitude of PEAK1 within each call (Figure E-3).

In RTS, cursor error was estimated to be ± 1 msec for time measurements and ± 15 Hz for frequency measurements. Cursor errors for power spectra in SIGNAL were estimated to be ± 0.1 dB-Volts and ± 15 Hz for amplitude and frequency measurements, respectively.

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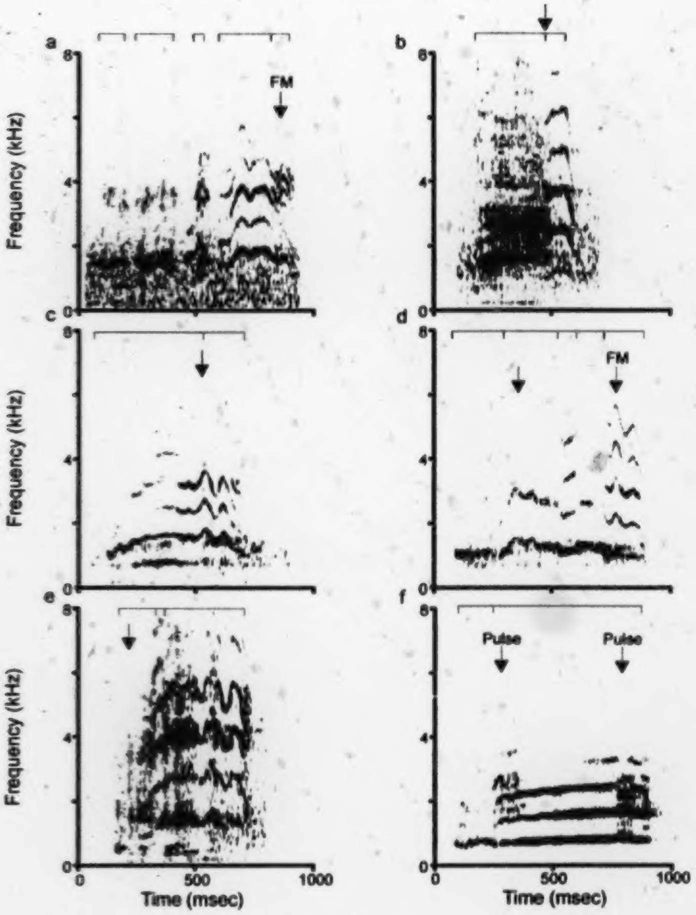


Figure E-1. Representative spectrograms (frequency bandwidth = 39 Hz) showing acoustic characteristics used to distinguish between call parts in this study. Horizontal bars designate call parts, arrows indicate features of interest.

a) 5-part call consisting of 3 pulses followed by a 2-part tonal section with frequency modulation.
b) 2-part call with abrupt change from pulsed to tonal quality.
c) 2-part tonal call with abrupt appearance of FM
d) 5-part tonal call with abrupt changes in harmonic interval, and FM in 2nd and 5th call parts.
e) 3-part call starting with a distinctly pulsed part that obscures underlying tonal structure.
f) 2-part call in which pulses are overlain but do not obscure tonal structure.

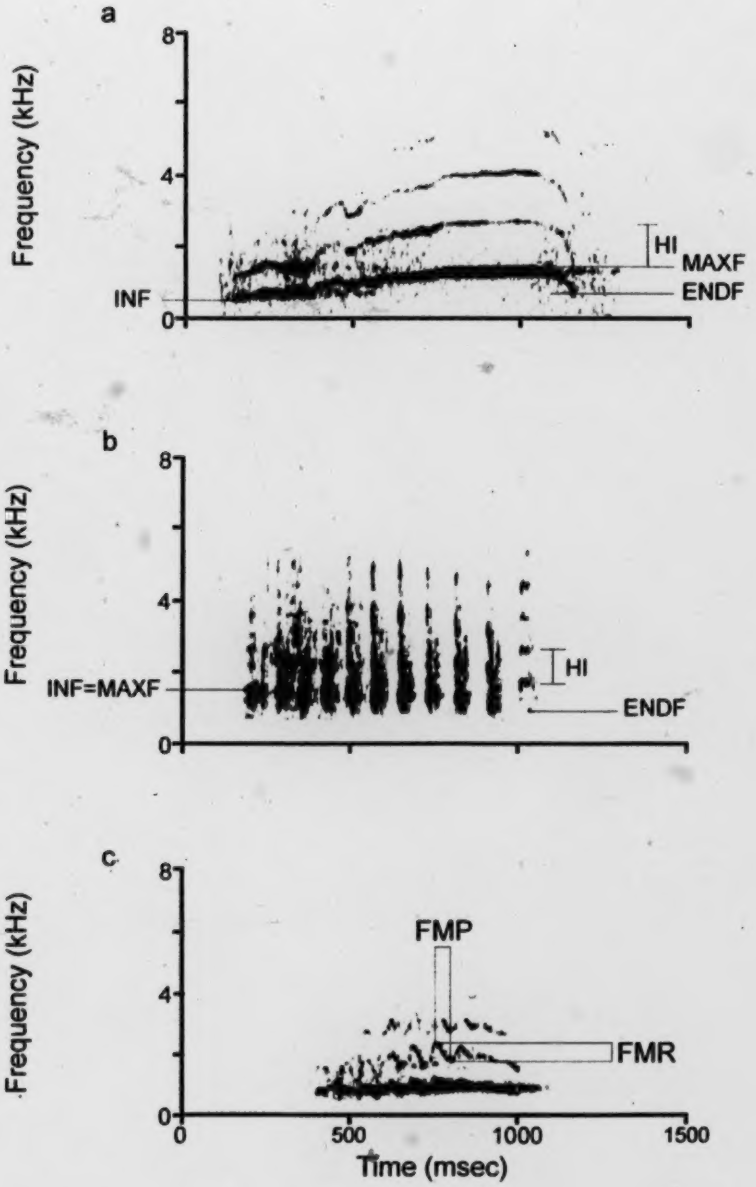


Figure E-2. Representative spectrograms showing measurement of frequency characteristics in this study. a) tonal call; b) pulsed call; c) measurement of frequency modulation. Frequency bandwidth = 39 Hz.

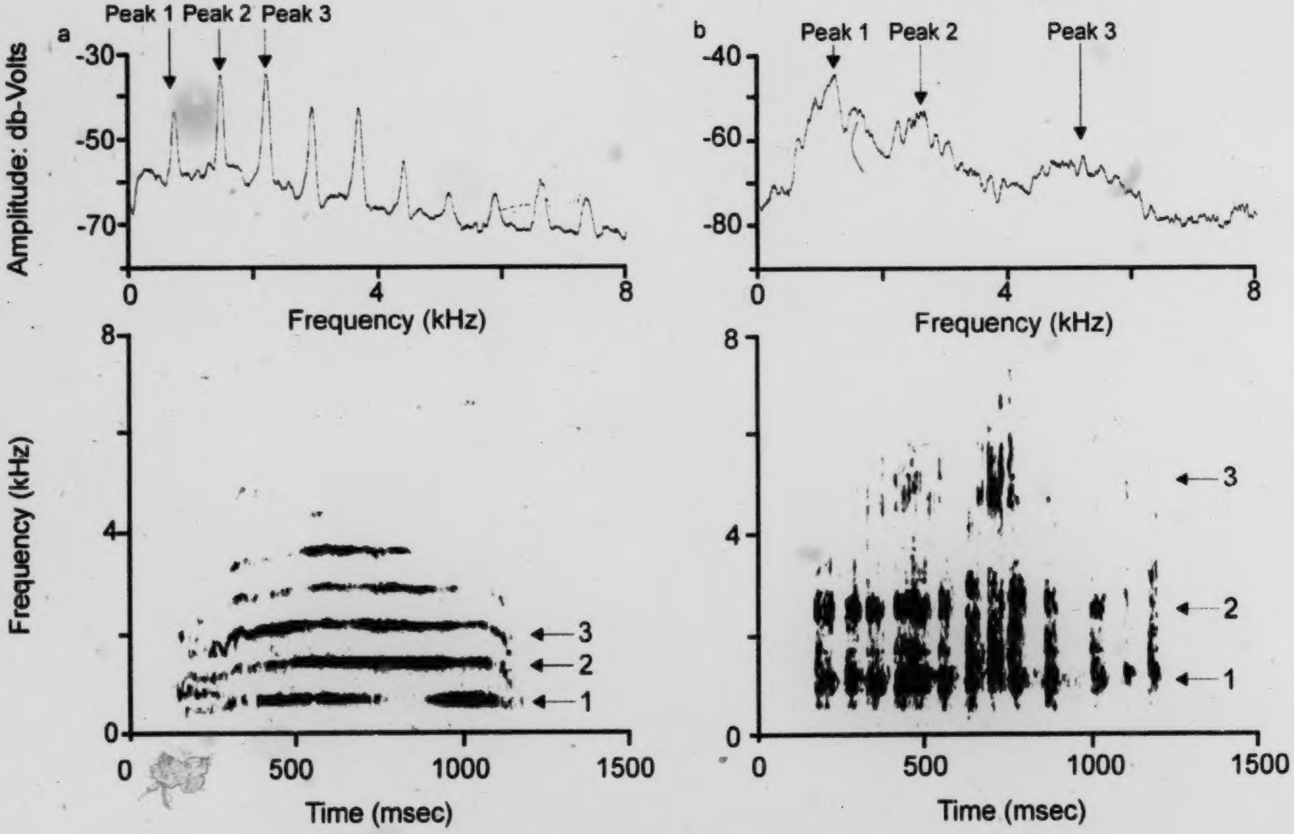


Figure E-3 Representative power spectra (upper) and spectrograms (lower) showing measurement of energy-emphasized frequency ranges in this study. a) tonal call in which energy peaks are harmonically related; b) pulsed call with wide energy bands. Frequency bandwidth of spectrograms = 39 Hz.

APPENDIX F

Summary statistics of acoustic variables and representative spectrograms of calls for each female and pup analyzed in Chapters 6 and 7.

SUMMARY STATISTICS - FEMALES

DUR

	Mean	S.E.	N	Min	Max
N408	1276	86.31	20	627	1975
N410	933	53.06	20	549	1354
N412	1107	67.80	20	560	1632
N418	910	49.75	20	597	1383
N434	1174	51.13	20	792	1581
N442	1249	54.32	20	864	1826
X72	885	37.80	20	684	1143
XX26F	750	39.95	20	361	1066
XX54	926	59.28	20	509	1717
XX58	810	26.81	20	632	1026
XX68	1553	73.51	20	1055	2231
XX70	1285	72.75	20	711	1904
XX77	767	30.22	20	540	1008
XX80	1158	41.81	20	853	1469
XX98	1071	55.10	20	702	1617
Group Total	1057	18.99	300	361	2231

NPARTS2

	Mean	S.E.	N	Min	Max
N408	1.43	.07	20	1.00	2.24
N410	1.60	.07	20	1.00	2.24
N412	1.73	.06	20	1.41	2.24
N418	1.54	.05	20	1.41	2.00
N434	1.68	.04	20	1.41	2.00
N442	1.02	.02	20	1.00	1.41
X72	1.96	.07	20	1.41	2.65
XX26F	1.45	.02	20	1.41	1.73
XX54	1.94	.05	20	1.41	2.24
XX58	1.57	.05	20	1.00	2.00
XX68	1.35	.04	20	1.00	1.73
XX70	1.35	.09	20	1.00	2.24
XX77	1.97	.08	20	1.41	2.65
XX80	1.87	.07	20	1.41	2.45
XX98	1.55	.05	20	1.41	2.24
Group Total	1.60	.02	300	1.00	2.65

NPARTS

	Mean	S.E.	N	Min	Max	Mode	Median
N408	2.15	.22	20	1	5	2	2
N410	2.65	.24	20	1	5	2	3
N412	3.05	.20	20	2	5	3	3
N418	2.40	.15	20	2	4	2	2
N434	2.85	.15	20	2	4	3	3
N442	1.05	.05	20	1	2	1	1
X72	3.95	.29	20	2	7	3	4
XX26F	2.10	.07	20	2	3	2	2
XX54	3.80	.19	20	2	5	4	4
XX58	2.50	.15	20	1	4	2	3
XX68	1.85	.11	20	1	3	2	2
XX70	1.95	.26	20	1	5	1	2
XX77	4.00	.32	20	2	7	5	4
XX80	3.60	.28	20	2	6	3	3
XX98	2.45	.17	20	2	5	2	2
Group Total	2.69	.07	300	1	7	2	2

INF

	Mean	S.E.	N	Min	Max
N408	906	28.82	20	630	1220
N410	723	16.80	20	590	840
N412	786	33.49	20	590	1310
N418	697	18.51	20	560	840
N434	721	16.84	19	590	840
N442	696	21.73	20	560	910
X72	761	16.52	20	660	910
XX26F	698	18.85	19	530	875
XX54	699	10.27	20	590	780
XX58	652	12.90	20	530	720
XX68	630	15.08	20	500	780
XX70	604	12.26	20	500	720
XX77	802	17.38	20	660	940
XX80	785	33.14	20	530	1060
XX98	757	16.94	20	630	910
Group Total	728	6.70	298	500	1310

MAXF

	Mean	S.E.	N	Min	Max
N408	1112	20.83	20	910	1280
N410	998	36.11	20	810	1410
N412	1189	37.27	20	880	1660
N418	914	19.47	20	810	1090
N434	903	22.16	20	720	1190
N442	804	28.16	20	560	1090
X72	833	9.74	20	780	910
XX26F	726	16.98	20	590	910
XX54	1017	40.42	20	780	1280
XX58	1287	18.64	20	1030	1380
XX68	749	12.85	20	660	880
XX70	720	6.16	20	660	780
XX77	1050	19.38	20	970	1280
XX80	916	15.29	20	780	1060
XX98	940	26.72	20	810	1220
Group Total	944	11.18	300	560	1660

ENDF

	Mean	S.E.	N	Min	Max
N408	811	22.90	20	630	1090
N410	773	35.02	20	630	1380
N412	928	16.40	20	780	1030
N418	739	16.12	20	590	840
N434	768	24.97	20	630	1190
N442	801	28.89	20	530	1090
X72	736	17.94	20	560	840
XX26F	612	9.55	20	560	690
XX54	823	12.92	20	750	1030
XX58	859	28.08	20	720	1190
XX68	742	14.37	20	630	880
XX70	692	7.69	20	630	750
XX77	989	19.42	20	880	1280
XX80	731	17.41	20	590	880
XX98	873	27.50	20	720	1160
Group Total	791	7.54	300	530	1380

HI

	Mean	S.E.	N	Min	Max
N408	1002	39.47	18	780	1250
N410	933	37.85	18	690	1220
N412	1097	46.98	19	840	1660
N418	927	19.41	20	780	1060
N434	855	13.85	20	750	1060
N442	.	.	0	.	.
X72	806	6.90	20	750	880
XX26F	690	10.22	20	590	750
XX54	913	43.00	20	530	1250
XX58	1275	19.73	20	1000	1410
XX68	744	10.27	20	680	840
XX70	722	5.54	20	690	750
XX77	991	22.95	20	720	1280
XX80	888	17.33	20	720	1000
XX98	843	20.59	16	750	1090
Group Total	905	11.38	271	530	1660

FMP

	Mean	S.E.	N	Min	Max
N408	.	.	0	.	.
N410	.	.	0	.	.
N412	36	6.43	8	16	63
N418	.	.	0	.	.
N434	17	2.70	7	9	32
N442	.	.	0	.	.
X72	.	.	0	.	.
XX26F	.	.	0	.	.
XX54	34	7.43	5	13	58
XX58	36	4.44	8	23	61
XX68	.	.	0	.	.
XX70	19	3.08	10	12	40
XX77	40	2.32	20	19	72
XX80	31	3.44	8	18	43
XX98	28	9.29	3	11	43
Group Total	31	1.70	69	9	72

FMR

	Mean	S.E.	N	Min	Max
N408	.	.	0	.	.
N410	.	.	0	.	.
N412	325	78.60	8	90	630
N418	.	.	0	.	.
N434	264	26.26	7	160	380
N442	.	.	0	.	.
X72	.	.	0	.	.
XX26F	.	.	0	.	.
XX54	184	27.50	5	130	250
XX58	294	55.48	8	130	590
XX68	.	.	0	.	.
XX70	193	12.21	10	130	250
XX77	627	42.76	20	310	1030
XX80	168	9.40	8	130	220
XX98	270	36.06	3	220	340
Group Total	353	27.58	69	90	1030

RESF1

	Mean	S.E.	N	Min	Max
N408	1009	33.18	20	830	1290
N410	926	30.71	20	700	1200
N412	1129	41.45	20	860	1510
N418	835	13.48	20	750	1000
N434	828	9.89	20	700	890
N442	822	21.41	20	640	1070
X72	778	8.11	20	740	890
XX26F	671	9.13	20	580	730
XX54	906	31.86	20	630	1200
XX58	1133	40.48	20	780	1340
XX68	716	12.64	20	630	820
XX70	700	7.96	20	640	770
XX77	938	14.62	20	780	1040
XX80	864	12.06	20	710	930
XX98	815	9.93	20	710	890
Group Total	871	9.74	300	580	1510

RESF2

	Mean	S.E.	N	Min	Max
N408	2076	111.14	18	1650	3580
N410	1935	71.40	20	1600	2830
N412	2081	72.68	20	1660	3000
N418	1667	49.16	20	1250	2010
N434	1659	26.38	20	1460	2060
N442	1603	74.33	20	1040	2600
X72	1564	13.81	20	1470	1730
XX26F	1362	24.51	20	1150	1580
XX54	1840	64.83	20	1270	2430
XX58	2136	72.34	20	1590	2600
XX68	1420	23.37	20	1220	1670
XX70	1399	13.47	20	1280	1510
XX77	1897	45.29	20	1660	2620
XX80	1794	52.32	20	1530	2690
XX98	1603	27.32	20	1380	1810
Group Total	1733	19.92	298	1040	3580

RESF3

	Mean	S.E.	N	Min	Max
N408	3349	122.84	14	2560	4440
N410	2761	100.11	19	1980	3940
N412	3090	121.93	17	2360	4160
N418	2518	115.24	18	1830	3520
N434	2671	106.85	19	2000	3450
N442	2899	282.29	17	1590	5870
X72	2958	152.94	20	2150	4350
XX26F	2091	44.03	20	1760	2640
XX54	2769	94.40	20	2270	3600
XX58	3285	132.99	20	2140	3870
XX68	2262	56.16	20	1900	2770
XX70	2126	26.91	20	1890	2430
XX77	2898	45.98	20	2490	3320
XX80	2782	119.42	20	2370	4770
XX98	2554	48.35	14	2240	2890
Group Total	2721	36.89	278	1590	5870

RAMP2

	Mean	S.E.	N	Min	Max
N408	69	2.82	18	46	88
N410	74	3.05	20	57	103
N412	85	2.13	20	74	109
N418	78	1.82	20	65	102
N434	77	1.78	20	64	94
N442	86	2.22	20	71	99
X72	86	2.81	20	66	110
XX26F	80	2.09	20	63	96
XX54	98	3.92	20	69	141
XX58	74	1.75	20	63	91
XX68	84	1.91	20	67	105
XX70	101	3.12	20	77	124
XX77	68	2.08	20	55	95
XX80	77	3.36	20	47	110
XX98	75	1.89	20	58	90
Group Total	81	.83	298	46	141

RAMP3

	Mean	S.E.	N	Min	Max
N408	59	2.55	14	47	78
N410	68	3.16	19	52	100
N412	73	2.28	17	58	92
N418	75	1.35	18	69	88
N434	61	1.58	19	50	75
N442	74	2.39	17	59	92
X72	64	1.29	20	54	73
XX26F	74	2.25	20	53	90
XX54	90	3.11	20	67	123
XX58	68	1.97	20	52	83
XX68	73	1.87	20	62	97
XX70	86	3.47	20	61	122
XX77	62	2.19	20	45	82
XX80	66	2.10	20	47	82
XX98	64	2.56	14	51	83
Group Total	71	.79	278	45	123

TONAL

	Mode	Median	N	Min	Max	# with
N408	1	1	20	1	1	20
N410	1	1	20	0	1	18
N412	1	1	20	0	1	19
N418	1	1	20	1	1	20
N434	1	1	20	1	1	20
N442	0	0	20	0	0	0
X72	1	1	20	1	1	20
XX26F	1	1	20	1	1	20
XX54	1	1	20	1	1	20
XX58	1	1	20	1	1	20
XX68	1	1	20	1	1	20
XX70	1	1	20	1	1	20
XX77	1	1	20	1	1	20
XX80	1	1	20	1	1	20
XX98	1	1	20	0	1	17
Group Total	1	1	300	0	1	274 (91.3 %)

FM

	Mode	Median	N	Min	Max	# with
N408	0	0	20	0	0	0
N410	0	0	18	0	0	0
N412	0	0	19	0	1	8
N418	0	0	20	0	0	0
N434	0	0	20	0	1	7
N442	.	.	0	.	.	.
X72	0	0	20	0	0	0
XX26F	0	0	20	0	0	0
XX54	0	0	20	0	1	5
XX58	0	0	20	0	1	8
XX68	0	0	20	0	0	0
XX70	0	1	20	0	1	10
XX77	1	1	20	1	1	20
XX80	0	0	20	0	1	8
XX98	0	0	17	0	1	3
Group Total	0	0	274	0	1	69 (25.2 %)

PULSE

	Mode	Median	N	Min	Max	# with
N408	0	0	20	0	1	4
N410	1	1	20	0	1	14
N412	1	1	20	0	1	17
N418	1	1	20	0	1	16
N434	1	1	20	0	1	19
N442	1	1	20	1	1	20
X72	1	1	20	1	1	20
XX26F	1	1	20	1	1	20
XX54	1	1	20	0	1	18
XX58	0	0	20	0	1	1
XX68	1	1	20	0	1	16
XX70	0	0	20	0	0	0
XX77	1	1	20	0	1	16
XX80	1	1	20	1	1	20
XX98	1	1	20	1	1	20
Group Total	1	1	300	0	1	221 (73.7 %)

SUMMARY STATISTICS – PUPS

DUR

	Mean	S.E.	Valid N	Min	Max
N403	773	37.48	20	453	1082
N407	801	40.49	20	436	1114
N409	545	34.39	20	276	825
N415	792	47.04	20	421	1262
N417	504	21.79	20	328	660
N433	576	35.62	20	237	1019
XX26	356	20.44	20	181	494
XX27	548	38.36	20	189	899
XX69	853	55.26	20	353	1225
XX71	437	30.51	20	243	735
XX73	552	35.35	20	364	976
XX75	482	35.09	20	316	920
XX99	578	48.05	20	230	1003
Group Total	600	13.87	260	181	1262

NPARTS2

	Mean	S.E.	N	Min	Max
N403	2.04	.09	20	1	3
N407	3.00	.09	20	2	3
N409	2.02	.09	20	1	3
N415	1.83	.05	20	1	2
N417	1.61	.09	20	1	2
N433	1.85	.07	20	1	2
XX26	1.60	.05	20	1	2
XX27	2.43	.07	20	2	3
XX69	3.10	.12	20	2	4
XX71	1.83	.07	20	1	3
XX73	2.46	.07	20	2	3
XX75	1.35	.07	20	1	2
XX99	1.72	.07	20	1	2
Group Total	2.06	.04	260	1	4

NPARTS

	Mean	S.E.	N	Min	Max	Mode	Median
N403	4.30	.34	20	1	7	4	4
N407	9.15	.49	20	5	12	10	10
N409	4.25	.39	20	2	8	3	4
N415	3.40	.17	20	2	5	3	3
N417	2.75	.29	20	1	5	2	2
N433	3.50	.25	20	2	5	4	4
XX26	2.60	.15	20	2	4	2	3
XX27	6.00	.36	20	3	10	7	6
XX69	9.90	.71	20	5	15	5	10
XX71	3.45	.28	20	2	7	3	3
XX73	6.15	.35	20	3	10	7	6
XX75	1.90	.19	20	1	4	2	2
XX99	3.05	.26	20	2	5	2	3
Group Total	4.65	.18	260	1	15	2	4

INF

	Mean	S.E.	Valid N	Min	Max
N403	1382	59.96	20	690	1750
N407	1236	29.16	20	1030	1610
N409	991	46.13	20	590	1340
N415	1058	28.87	20	840	1310
N417	1131	59.93	20	780	2000
N433	1201	56.49	19	810	1590
XX26	1371	40.73	20	1130	1840
XX27	1275	32.11	20	1000	1630
XX69	1377	30.06	20	1090	1690
XX71	1131	36.96	20	880	1440
XX73	1183	29.04	20	970	1470
XX75	867	49.34	20	590	1380
XX99	1172	50.19	19	880	1720
Group Total	1182	14.99	258	590	2000

MAXF

	Mean	S.E.	Valid N	Min	Max
N403	1735	61.36	20	910	1970
N407	1403	31.31	20	1140	1830
N409	1175	48.23	20	880	1530
N415	1387	40.93	20	1060	1560
N417	1290	54.19	20	1000	2090
N433	1448	58.89	20	1060	2160
XX26	2119	94.62	20	1340	2630
XX27	1490	37.80	20	1280	1910
XX69	1567	18.45	20	1380	1690
XX71	1393	71.11	20	910	2000
XX73	1503	21.34	20	1310	1660
XX75	1107	51.48	20	750	1630
XX99	1499	74.88	20	1220	2500
Group Total	1470	21.29	260	750	2630

ENDF

	Mean	S.E.	Valid N	Min	Max
N403	1435	61.63	20	720	1720
N407	1319	35.02	19	1030	1580
N409	1039	59.83	20	590	1380
N415	1153	34.29	20	910	1440
N417	1080	53.06	20	810	1810
N433	1158	52.94	20	780	1530
XX26	1618	76.59	20	970	2190
XX27	1387	53.20	20	750	1810
XX69	1442	35.60	20	1060	1690
XX71	1222	61.06	20	780	1630
XX73	1390	33.07	20	1090	1660
XX75	852	40.50	20	660	1310
XX99	1194	53.07	19	880	1750
Group Total	1253	18.65	258	590	2190

HI

	Mean	S.E.	Valid N	Min	Max
N403	853	49.66	18	410	1380
N407	998	93.93	4	720	1130
N409	704	75.52	8	410	910
N415	1158	32.91	20	940	1410
N417	1080	30.03	19	750	1250
N433	1186	40.56	20	810	1440
XX26	1110	35.68	20	750	1340
XX27	838	125.12	4	470	1030
XX69	.	.	0	.	.
XX71	850	82.14	6	470	1000
XX73	689	13.88	12	590	751
XX75	934	35.63	20	660	1190
XX99	1206	30.81	20	910	1410
Group Total	1018	17.78	171	410	1440

FMP

	Mean	S.E.	Valid N	Min	Max
N403	48	3.64	17	19	77
N407	41	7.42	3	32	56
N409	32	1.76	3	29	35
N415	57	5.36	15	32	98
N417	38	2.86	13	15	54
N433	45	4.59	15	20	81
XX26	.	.	0	.	.
XX27	187	.	1	187	187
XX69	.	.	0	.	.
XX71	.	.	0	.	.
XX73	27	.	1	27	27
XX75	31	2.59	11	15	45
XX99	32	2.78	16	14	55
Group Total	43	2.29	95	14	187

FMR

	Mean	S.E.	Valid N	Min	Max
N403	353	36.08	17	160	720
N407	361	151.35	3	172	660
N409	137	29.06	3	90	190
N415	297	39.02	15	60	690
N417	268	53.56	13	90	780
N433	427	111.61	15	90	1910
XX26	.	.	0	.	.
XX27	530	.	1	530	530
XX69	.	.	0	.	.
XX71	.	.	0	.	.
XX73	380	.	1	380	380
XX75	175	20.47	11	60	280
XX99	487	39.24	16	220	840
Group Total	342	24.39	95	60	1910

RESF1

	Mean	S.E.	Valid N	Min	Max
N403	1561	39.77	20	990	1740
N407	1266	33.62	20	870	1460
N409	1146	40.98	20	850	1440
N415	1202	27.67	20	1000	1440
N417	1331	65.21	20	990	2260
N433	1346	42.37	20	1040	1620
XX26	1528	44.39	20	1140	2040
XX27	1404	35.12	20	1040	1600
XX69	1466	12.32	20	1300	1540
XX71	1405	55.53	20	1020	1980
XX73	1409	20.90	20	1290	1590
XX75	1387	34.48	20	1080	1660
XX99	1285	35.77	20	880	1670
Group Total	1364	12.94	260	850	2260

RESF2

	Mean	S.E.	Valid N	Min	Max
N403	3663	76.58	20	2820	4510
N407	2360	93.20	20	1450	3510
N409	2778	68.12	20	2160	3590
N415	2796	74.56	20	1990	3380
N417	2570	123.71	20	1920	3910
N433	2806	133.04	20	1860	3960
XX26	2624	64.61	20	2140	3170
XX27	2845	139.04	20	1780	3740
XX69	2921	68.96	20	2350	3570
XX71	2906	80.18	20	2120	3330
XX73	2965	74.73	20	2080	3530
XX75	2757	108.69	20	2040	3570
XX99	2725	96.20	20	2180	3750
Group Total	2824	31.50	260	1450	4510

RESF3

	Mean	S.E.	Valid N	Min	Max
N403	4705	108.14	14	4180	5480
N407	3387	107.10	20	2960	5150
N409	5200	156.61	17	4090	6080
N415	4075	120.70	20	2980	4900
N417	3751	134.60	20	2960	5390
N433	3961	152.92	20	3000	5270
XX26	3778	116.27	19	3020	4510
XX27	3992	133.41	20	3230	5160
XX69	4629	98.89	20	3250	5380
XX71	4047	139.71	20	2980	5200
XX73	4553	80.36	19	4020	5410
XX75	4098	165.79	20	3020	5510
XX99	4018	132.74	20	3270	5130
Group Total	4143	45.25	249	2960	6080

RAMP2

	Mean	S.E.	Valid N	Min	Max
N403	88	2.46	20	68	107
N407	82	1.96	20	68	103
N409	73	2.75	20	56	105
N415	78	3.00	20	58	114
N417	94	3.86	20	60	130
N433	90	2.95	20	63	113
XX26	92	2.61	20	65	111
XX27	86	1.75	20	76	113
XX69	86	1.82	20	69	103
XX71	91	2.62	20	68	112
XX73	84	2.25	20	64	99
XX75	92	3.13	20	50	112
XX99	86	2.36	20	60	108
Group Total	86	.80	260	50	130

RAMP3

	Mean	S.E.	Valid N	Min	Max
N403	80	2.84	14	57	100
N407	83	2.22	20	68	102
N409	65	2.40	17	46	80
N415	69	2.26	20	51	92
N417	107	5.48	20	60	173
N433	97	3.22	20	68	117
XX26	82	2.51	19	60	99
XX27	83	1.79	20	65	99
XX69	79	1.43	20	64	89
XX71	88	2.74	20	68	113
XX73	73	2.20	19	53	91
XX75	84	3.88	20	52	132
XX99	85	2.62	20	62	101
Group Total	83	1.04	249	46	173

TONAL

	Mode	Median	N	Min	Max	# with
N403	1	1	20	0	1	18
N407	0	0	20	0	1	4
N409	0	0	20	0	1	8
N415	1	1	20	1	1	20
N417	1	1	20	0	1	19
N433	1	1	20	1	1	20
XX26	1	1	20	1	1	20
XX27	0	0	20	0	1	4
XX69	0	0	20	0	0	0
XX71	0	0	20	0	1	6
XX73	1	1	20	0	1	12
XX75	1	1	20	1	1	20
XX99	1	1	20	1	1	20
Group Total	1	1	260	0	1	171

(65.5 %)

FM

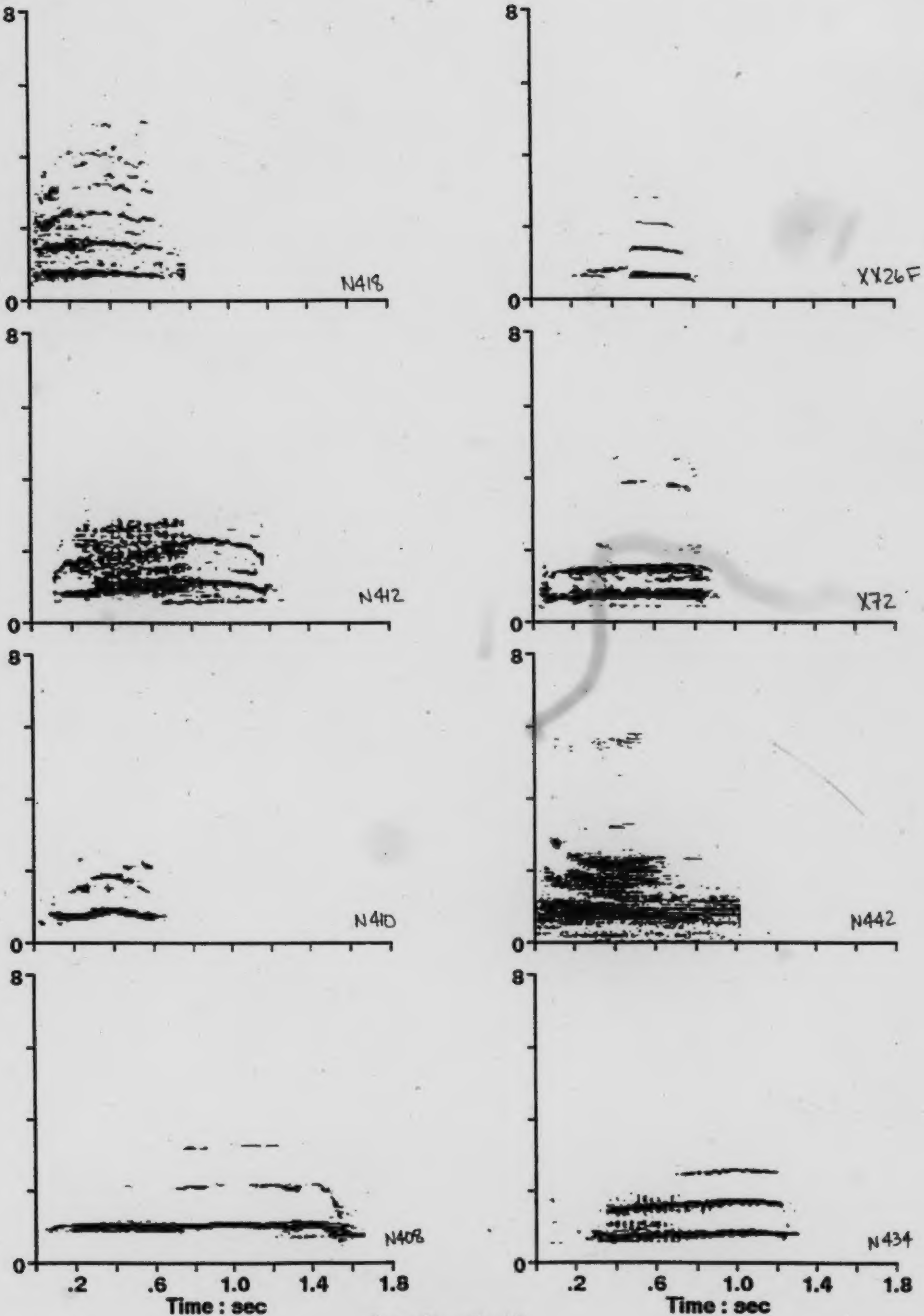
	Mode	Median	N	Min	Max	# with
N403	1	1	18	0	1	17
N407	1	1	4	0	1	3
N409	0	0	8	0	1	3
N415	1	1	20	0	1	15
N417	1	1	19	0	1	13
N433	1	1	20	0	1	15
XX26	0	0	20	0	0	0
XX27	0	1	4	0	1	2
XX69	.	.	0	.	.	.
XX71	0	0	6	0	0	0
XX73	0	0	12	0	1	1
XX75	1	1	20	0	1	11
XX99	1	1	20	0	1	16
Group Total	1	1	171	0	1	96

(56.1 %)

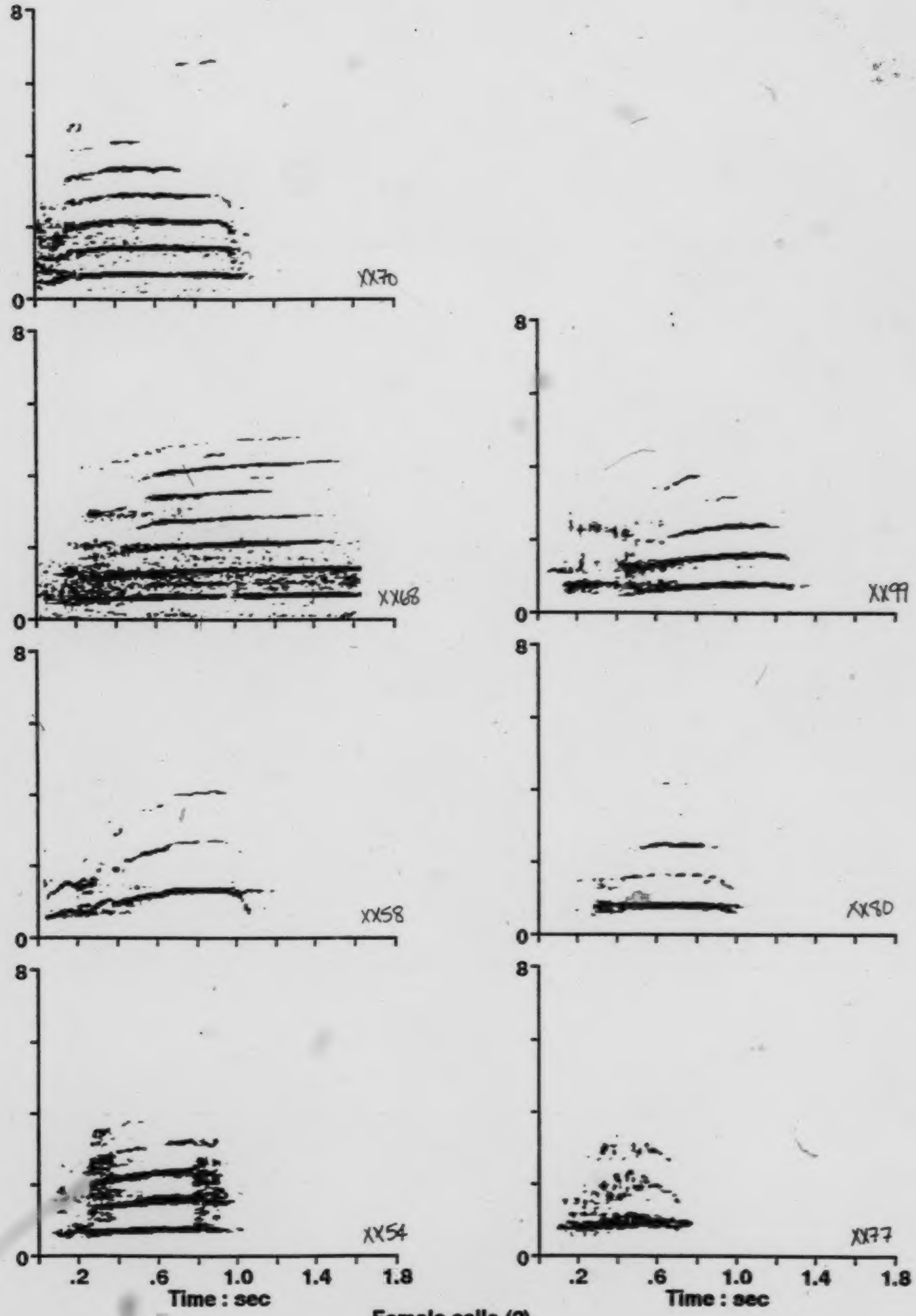
PULSE

	Mode	Median	N	Min	Max	# with
N403	1	1	20	0	1	17
N407	1	1	20	1	1	20
N409	1	1	20	0	1	19
N415	1	1	20	0	1	12
N417	1	1	20	0	1	13
N433	1	1	20	1	1	20
XX26	1	1	20	1	1	20
XX27	1	1	20	1	1	20
XX69	1	1	20	1	1	20
XX71	1	1	20	1	1	20
XX73	1	1	20	1	1	20
XX75	0	0	20	0	1	9
XX99	1	1	20	0	1	18
Group Total	1	1	260	0	1	228

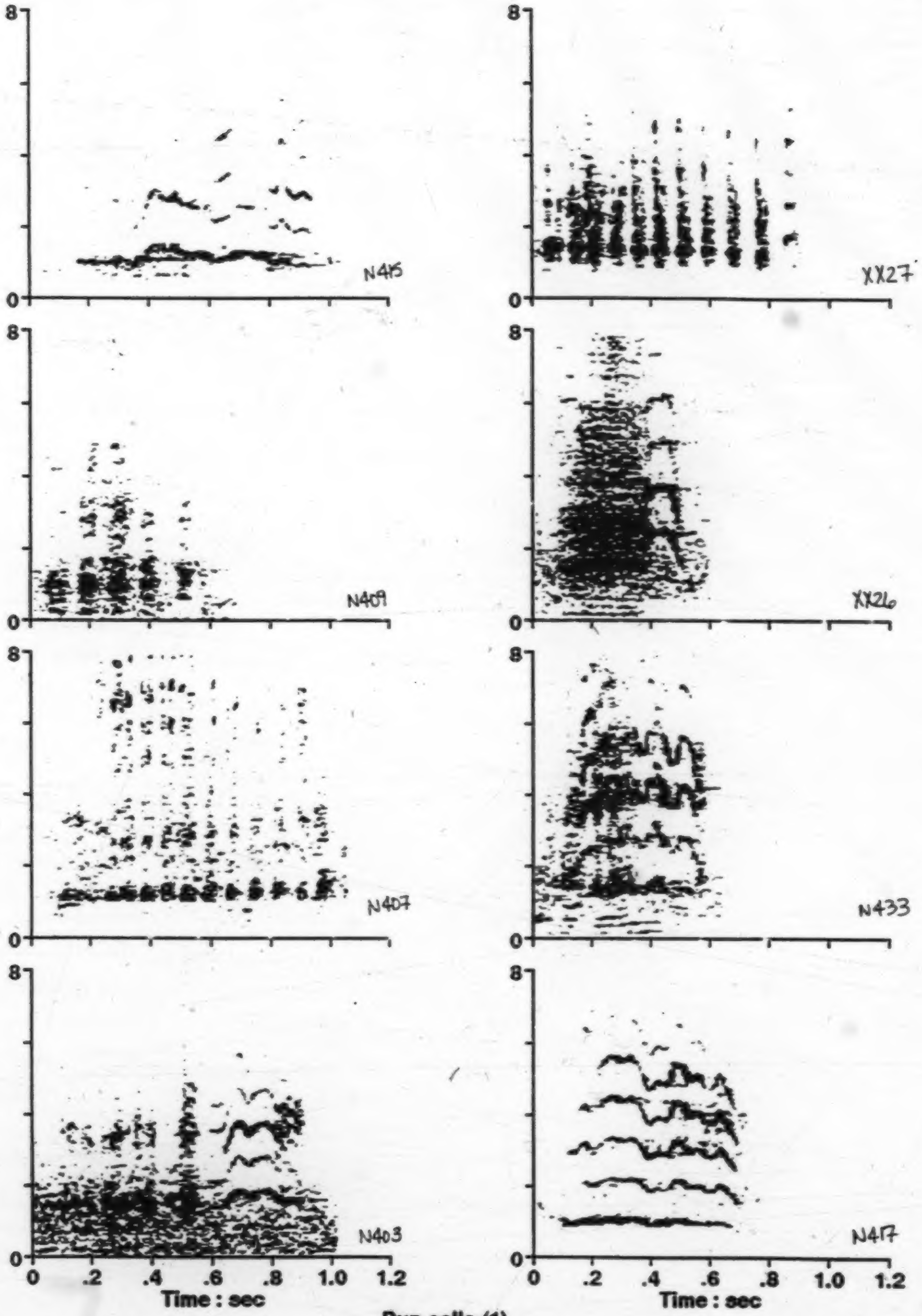
(87.7 %)



Female calls (1)



Female calls (2)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XX27
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N409
8
0
XX26
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N407
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N403
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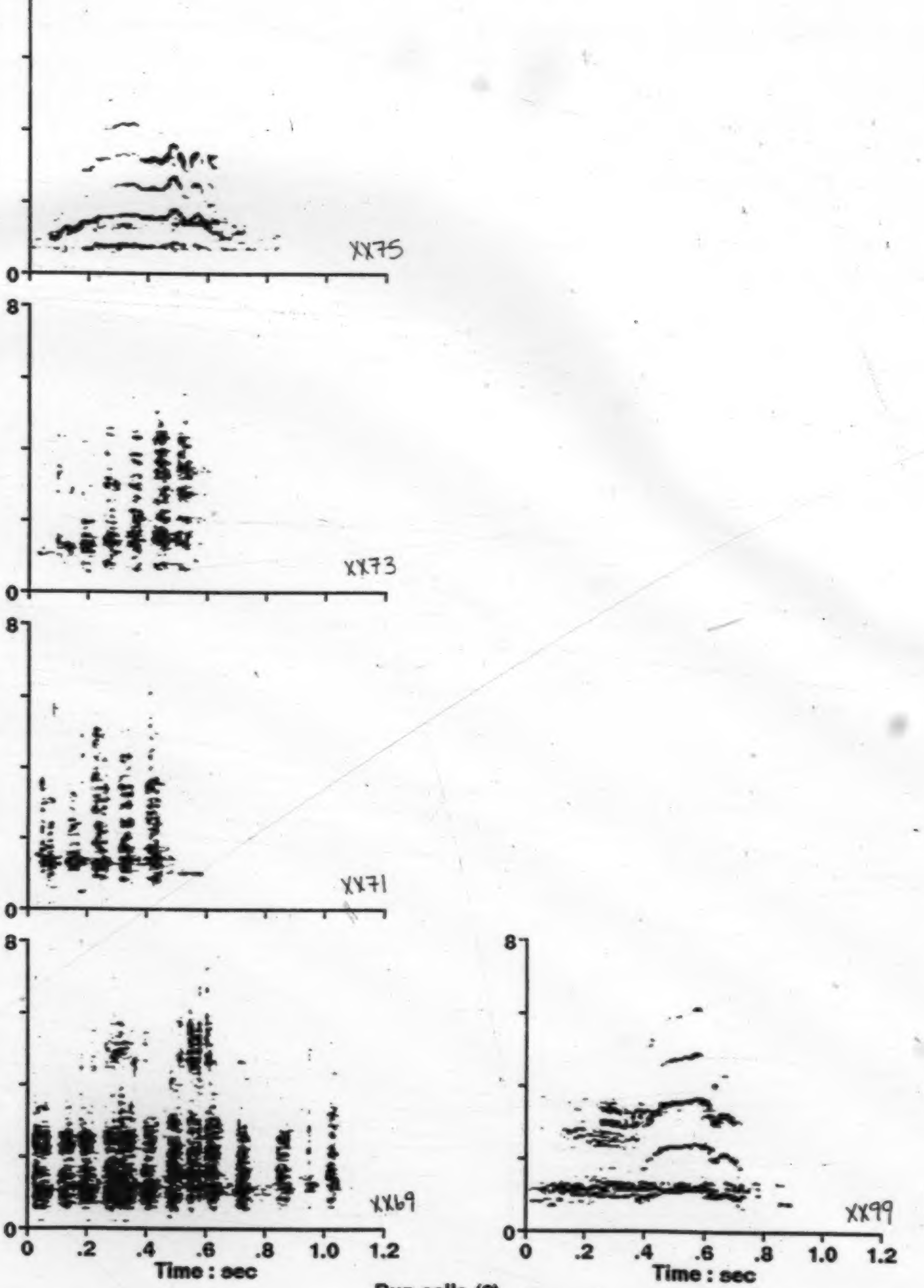
.8
1.0
1.2
Time : sec
0
.2
.4
.6
.8
1.0
1.2
Time : sec

Pup calls (1)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XX71
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XX69
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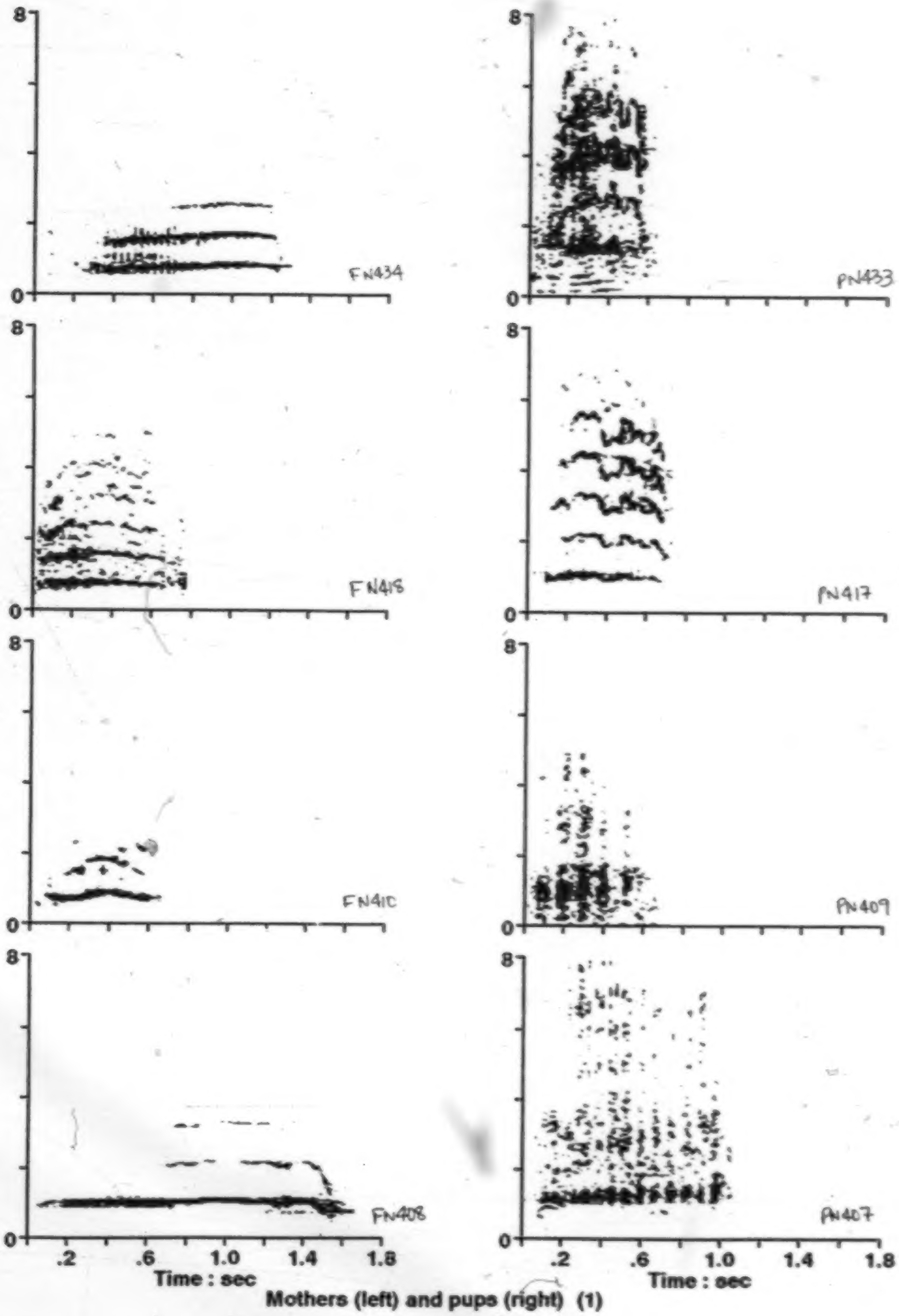
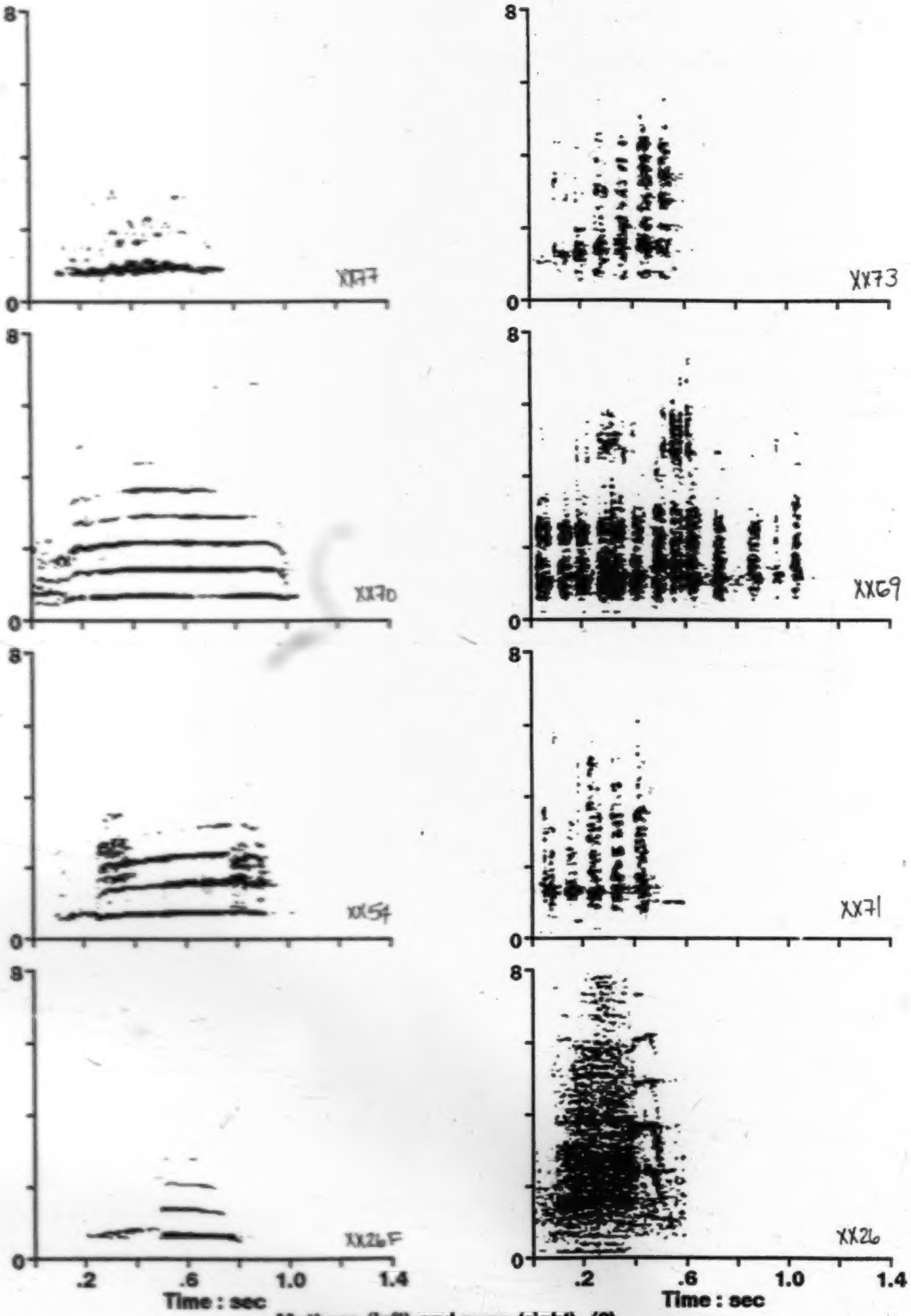
1.0
1.2
Time : sec
8
0
XX99
0
.2
.4
.6
.8
1.0
1.2
Time : sec

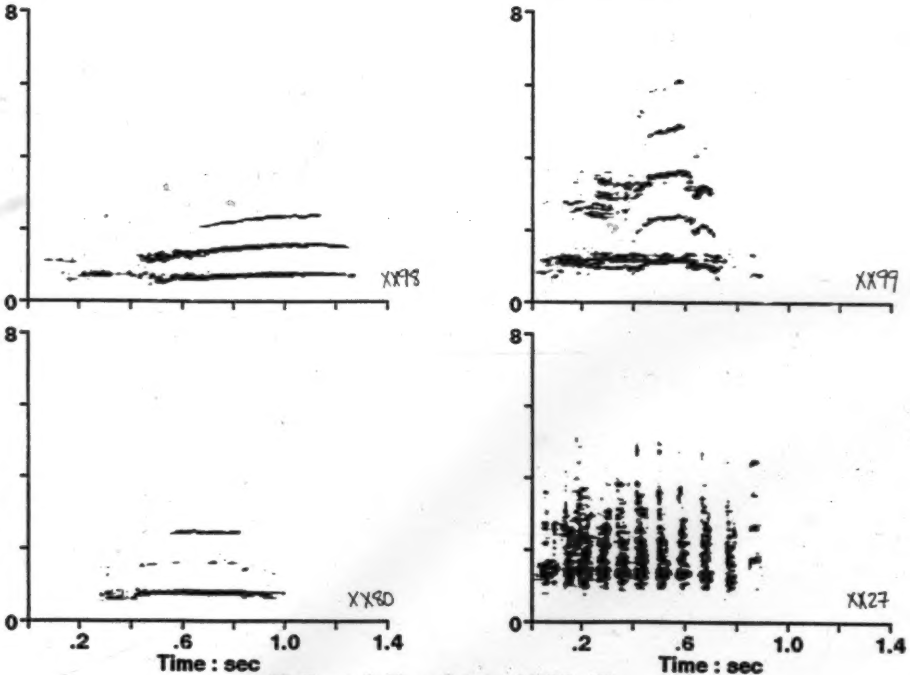
Pup calls (2)



Mothers (left) and pups (right) (1)



Mothers (left) and pups (right) (2)



Mothers (left) and pups (right) (3)